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A COMPARISON OF BIOTIC COMMUNITIES OF THE CEDAR-HEMLOCK AND OAK-HICKORY ASSOCIATIONS

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INTRODUCTION

Scope of the Problem

More than a score of ecologists have published comprehensive papers concerning biotic land communities in diverse parts of North America. Tundra (Shelford & Twomey 1941), grassland (Shackleford 1929, Carpenter 1940; *et al.*), beech-maple climax forest (Williams 1936), Maine coniferous forest (Blake 1926), Arizona desert-grassland (Vorhies & Taylor 1922, Taylor & Loftfield 1924, Greene & Reynard 1932), and various other communities have been investigated. Some of these accounts have emphasized seral stages in community development, others have offered a unique feature in the presentation of complex food chains involving many of the organisms within the community, and all have made noteworthy contributions to our knowledge of the biotic communities of the continent. However, these publications almost without exception have presented descriptions of community organization primarily rather than expositions of dynamic processes by comparison of different major communities.

In view of these facts, the chief objective of this paper will be to delineate and compare the principal dynamic processes involved in two major forest communities; action and response, reaction, coaction, aspection, and annuation will be considered. A comparison of two communities investigated by the author strengthens the discussion of community dynamics.

Orientation of the Communities

The communities considered are widely separated geographically. One, a Douglas fir-hemlock forest, is a late subclimax stage in the development of the Cedar-Hemlock Association. This association is the most extensive one in the Moist Coniferous Forest Biome of the Pacific Northwest and includes the forest communities throughout the moister and cooler parts of the region between the Cascade Mountains and the coastal "fog belt" in Oregon and Washington. In it western hemlock (*Tsuga heterophylla* Sarg.), western red cedar (*Thuja plicata* D. Don.), and true firs (*Abies* spp.) dominate (Munger 1927, 1940, Isaac 1938, 1940; *et al.*).

The area of coniferous forest studied was situated in the Oregon Coast Range at an average elevation of 1400 feet on the north side of Saddle Mountain in northeastern Lincoln County, Oregon (Fig. 1). While much of the forest on Saddle Mountain has been traversed by the writer, an area of approximately two hectares—which will be referred to as the "research station"—formed the center of intensive investigation.

FIG. 1. Interior of the Douglas fir-hemlock community, showing size of trees and typical forest floor cover with scattered sword fern, Oregon grape, and salal occurring in patches of herbaceous growth.

A count of all the trees in one hectare showed the presence of 75 Douglas firs (*Pseudotsuga taxifolia* Britt.) ranging in estimated height from about 180 to 230 feet and averaging 4 to 5 feet in diameter, 80 hemlocks about 130 to 170 feet in height (the tops reaching the lower branches in the Douglas fir crowns) and averaging 2 to 3 feet in diameter, and 2 noble firs (*Abies nobilis* Lindl.) about 4.5 feet in diameter and 200 feet in height. Beneath the larger trees there is an uneven-aged stand of young hemlocks ranging in height from 2 or 3 feet up to the crowns of the larger trees. Young trees are frequently clustered in almost pure stands, averaging 10 to 20 feet in height and producing such dense shade that little or no vegetation can persist beneath them. In the station hectare there were 530 of these young hemlocks over 3 feet in height (Fig. 2).

In the Douglas fir-hemlock community the shrub layer consists of widely scattered aggregations of huckleberry plants (*Vaccinium ovalifolium* Smith and *V. parvifolium* Smith) which alternate with the

Fig. 2. Interior of the Douglas fir-hemlock forest, showing shrub layer of sword fern and salal in the foreground and a clump of young hemlock trees in the background, representative of station hectare.

lower Oregon grape (*Berberis nervosa* Pursh.), salal (*Gaultheria shallon* Pursh.), and sword fern (*Polystichum munitum* (Kaulf.) Presl.). Even these lower shrubs do not form a continuous layer but frequently are rather widely spaced and "patchy" in occurrence. All of these shrubs, with the exception of the huckleberries which are seasonal, are evergreen and perennial. The plants of the herb layer are principally seasonal in occurrence, the most common ones occurring during the summer months being vanilla-leaf (*Achlys triphylla* (Smith) D. C.), wood sorrel (*Oxalis oregona* Nutt.), wood rush (*Juncoides parviflorum* (Ehrl.) Coville), and clintonia (*Clintonia uniflora* (Schult.) Kunth.). Areas in which the herbs occur are rather widely spaced, alternating with shrubby areas, and are almost exclusively beneath openings in the tree canopy. Frequently, however, scattered low fern and salal plants grow among the herbs (Fig. 1).

The forest floor is carpeted with a mat of several species of mosses where a dense growth of young hemlocks, shrubs, or herbs does not inhibit their growth. The two most common species are *Rhytidiadelphus loreus* (L. Hedw.) Wainst. and *Hylocomium splendens* (Hedw.) Bry. Eur. This mat of

mosses averages approximately 6 cm. in thickness though it is heavier in restricted areas. Logs, snags, and branches are common and contribute greatly to the amount of humus. Logs in advanced stages of decomposition are usually covered with the moss layer, and it is not an infrequent occurrence to find fallen Douglas firs four feet or more in diameter with moss and young hemlock trees several feet tall growing on them. Subsequent logging operations have revealed that many of these logs are still sound though they have been down for a number of years while some of the trees which were standing when this study was made have no commercial value.

As nearly as can be concluded from personal observation and literature on the subject, this community compared favorably with other mature or overmature Douglas fir-hemlock forests of the region. The forest at the time of this study was uninterrupted for many miles and was contiguous with the other forest communities of the Coast Range. It was in all respects primitive and unaffected by the presence of man. Saddle Mountain has since been logged.

The second community investigated is a representative fragment of the Oak-Hickory Association, the westernmost climax in the Eastern Deciduous Forest Biome. Since this association borders the Grassland Biome on the west, it is the deciduous forest association with the lowest effective rainfall. The trees in it are all species with comparatively low moisture requirements. Climax forests of the association extend farthest east on glacial plains of the prairie peninsula, and subclimax representatives are found on dry slopes and the tops of ridges throughout the Appalachian plateaus (Braun 1938). The Oak-Hickory Association also extends southward into the Ouchita and Ozark region of Oklahoma (Bruner 1931). Apparently no quantitative studies of this association have been made previous to the one recorded in this paper.

The woodlands which occupied a much more extensive portion of the area of this region in pioneer days have become restricted to isolated groves and woodlots at the present time. Man with his extensive farming activities has greatly modified the virginal condition, for he has extirpated most of the large mammals from the region (Cory 1912, Wood 1910). There is also a marked tendency for insect pests of cultivated plants to migrate into the woods from nearby fields and modify the dynamics of the communities still further (Weese 1924; *et al.*).

The oak community studied by the writer is a privately owned tract with an area of approximately 5.2 hectares and is situated about 20 miles west of Urbana, near White Heath, Piatt County, Illinois. The area represents a characteristic upland woods. It is separated from the forest of the Sangamon River floodplain on the north by a cultivated field about 100 meters in width. There is another cultivated field on the east, a pasture on the south, and a road on the west. In the southeast corner there is a fenced area of about 1.2 hectares in which livestock are permitted and in which there is a dense growth of

shrubs; this portion was not included in the present study. The remaining 4 hectares have been protected from grazing and browsing by livestock and have been relatively undisturbed for a number of years. The woodland is rectangular in shape and approximately four times as long as wide with the long axis in an east-west direction. The difference in elevation throughout the woods does not amount to more than a few feet.

The dominant trees of this community in order of abundance are white oak (*Quercus alba* L.), red oak (*Q. borealis maxima* Ashe), American elm (*Ulmus americana* L.), slippery elm (*U. fulva* Michx.), black oak (*Quercus velutina* Lam.), black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Erh.), bitternut hickory (*Carya cordiformis* K. Koch), and shagbark hickory (*C. ovata* K. Koch). The abundance of these species has been determined by counting the trees in one-fourth or one-half acre plots with supplementary strip counts in the center and east and west ends of the woods. The trees in the oak community average about two feet in diameter and 70 to 75 feet in height (Fig. 3).

Plant species which are represented by the greatest number of individuals in the shrub layer of the oak community are undoubtedly the American and slippery elms, for seedlings of these two species form an extensive lower story beneath the canopy of the taller trees, ranging in height from about five feet up to the lower branches in the crowns of the larger trees. Interspersed at rather frequent intervals throughout the woods are also smaller plants of elder (*Sambucus canadensis* L.), burning bush (*Euonymus atropurpureus* Jacq.), gooseberry (Ribes sp.), and several species of Crataegus. Seedlings of shagbark and bitternut hickory, linden (Tilia sp.), black cherry, mulberry (*Morus rubra* L.), hackberry (*Celtis occidentalis* L.), and oaks are not uncommon. Along the south edge of the woods where the shrub layer is heaviest, crab (Pyrus sp.), coralberry (*Symphoricarpos orbiculatus* Moench.), and one or more species of Viburnum are conspicuous elements though coralberry is found commonly along all the edges of the woods. The herb society changes so radically from season to season that it is difficult to characterize it. Spring beauty (*Claytonia virginica* L.), violets (*Viola pubescens* Ait. and *V. papilionacea* Pursh.), toothwort (*Dentaria laciniata* Muhl.), squirrel corn (*Dicentra canadensis* (Goldie) Walp.), and Dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.) of the early part of the prevernal season are followed by trillium (*Trillium recurvatum* Bec.), Jack-in-the-pulpit (*Arisaema triphyllum* (L.) Schött.), Solomon's seal (*Polygonatum commutatum* (R. & S.) Dietr.), false Solomon's seal (*Smilacina stellata* (L.) Desf.), mandrake (*Podophyllum peltatum* L.), and others, which usher in the vernal season. Jewelweed (*Impatiens biflora* Walt.) is a conspicuous plant of the summer months, while in the autumnal season, the white

Fig. 3. Interior of the oak woods. Picture was taken in the early fall and shows the absence of herbage at that time. Typical heavy growth of shrubs is conspicuous in the background.

snake-root (*Eupatorium urticaefolium* Reichard) is
the only common herb in evidence.

The forest floor is covered with a mat of fallen
leaves and dead herbaceous plants throughout the
year. This varies in thickness from approximately
6 cm. in the autumn shortly after leaf fall (Fig. 4)
to about 2 or 3 cm. in the prevernal season after
the leaves have been compressed by rain and snow.
A relatively small percentage of the area of the
forest floor is covered by logs in various stages of
decomposition.

PERIOD AND METHOD OF INVESTIGATION

Field studies in the Douglas fir-hemlock community
were made throughout the summers of 1935 to 1938,
inclusive. The area was visited at least once a month
during June, July, and August each of these years.
In addition over a period of several years, the author
had occasion to visit the coniferous forest community
many times including every season and thus has a
greater familiarity with the community than this sum-
mer study alone indicates. In the oak community
field studies were made at weekly, biweekly, or
monthly intervals—depending upon the weather—
from October 24, 1937, to April 2, 1940.

The methods employed in making the field investi-
gations in the two communities were similar in all
essential respects.

Invertebrate Populations. In both communities
the sweep net method of sampling was used for de-
termining the invertebrate populations in the herb
and shrub layers. Since previous investigators (Da-
vidson 1932, Jones 1946, Rice 1946, Shelford &
Twomey 1941; *et al.*) have considered 48-50 strokes
made with a 30 cm. net as covering approximately
one square meter of vegetation, the author selected
this unit as a standard. Use of this square meter
unit made possible the comparison of results obtained
in these two communities and will facilitate com-
parison of these results with ones secured by other
workers.

During the period from 1935 through 1937, the
animals occurring in the lower branches of the young
hemlock trees of the coniferous forest community
were studied by the sweep net method. However,
the accuracy of this method is doubtful because of
the nature of the vegetation, and in the summer of
1938 a white "beating cloth" was substituted. This
consisted of a heavy cloth one meter square attached
to a collapsible wooden frame. The cloth was placed
beneath several small hemlock branches which were
struck with a number of hard, quick blows. This
method proved effective in dislodging spiders, larvae,
and any adult insects present.

Consistent quantitative collections from the tree
tops were impossible because of the inaccessibility of
the layers. In the Douglas fir-hemlock community
occasional semiquantitative collections were made in
the crown of a 150 foot hemlock up which a ladder

FIG. 4. Detail of the forest floor of the oak community in early autumn, showing the heavy carpet of decidu-
ous tree leaves.

had been constructed to the 80 foot level where branches began.

For both communities the unit used for the humus and soil samples was 0.1 square meter, taken to a depth of 10 cm. Usually the sample was inspected in the laboratory since more careful counts of animals could be made in that way. For the oak community studies, a modified Berlese funnel was used to dry the humus and leaf litter portion of the samples from May 20, 1939, to the end of the study. For smaller organisms this was more nearly accurate than manual sorting. Quantitative samples from the ground layer were taken every time either community was visited with the exception of the year 1935 for the Douglas fir-hemlock community.

Some of the more common and more easily recognized invertebrates have been identified by the writer in the field or in the collections taken to the laboratory. The greater portion of the material collected, however, has been preserved and sent to specialists for determination As a result, the identifications should be entirely reliable. The numerous individuals who have aided in this phase of the work are listed in the acknowledgments.

Bird and Mammal Populations.—The methods of conducting bird censuses in the two communities differed somewhat. In the oak community an attempt was made to obtain as nearly complete an estimate as possible of the birds present in the entire woods (approximately 4 hectares). This was done by walking from one end of the woods to the other through several parallel strips, recording all birds seen or heard in the strips under observation. Field identifications were made by the writer and helpers. Owing to the great size of the Douglas fir-hemlock community, a census of one of the "station" hectares was kept as indicative of the bird population. Field identification of birds in this community was made by the writer; however, in most cases of uncertainty, birds were collected for identification by Mr. Stanley G. Jewett.

No quantitative mammal trapping was undertaken in the Douglas fir-hemlock community though small areas were trapped intensively for one or two nights on several occasions. Identification of the mammals obtained has been verified by Mr. Stanley G. Jewett. In the oak community a 0.5 acre circular plot located near the center of the woods was trapped with "killer" traps in November of each year. In 1939 two additional 0.25 acre circular areas were trapped in a similar manner; one of these was in the higher and drier east end of the woods; the other was in the lower, damper, and more brushy west end.

Meteorological Records.—Meteorological data are essential to a complete understanding of the organisms in a community, and in the case of both of these communities the writer recorded as completely as possible the weather conditions at the time each field study was made. The data used for the Oregon Douglas fir-hemlock community are from records obtained in the forest community on Saddle Mountain during the years 1934 through 1937 by Professor James A. Macnab then of Linfield College. However, the author's records for the oak community and those secured by the U. S. Weather Bureau station maintained on the campus of the University of Illinois at Urbana are so similar that the latter—being more complete—have been utilized for this paper.

A grant from the Graduate School of the University of Illinois aided in the preparation of specimens and other routine tasks.

COMPARISON OF THE DYNAMICS OF THE TWO BIOTIC COMMUNITIES

The major activities within biotic communities may be summed up in three groups of dynamic processes: (1) *action* of the habitat upon the associated organisms and *response* to this action, (2) *reaction* of the community constituents upon the various physical conditions which comprise the habitat, and (3) *co-action* of the organisms upon one another. *Aspection* and *annuation* are additional community functions which express combinations of the three primary activities. Any true comparison of biotic communities must be a consideration of these functions. (The terminology used in this paper is in agreement with that used in "Bio-ecology," Clements & Shelford 1939.)

ACTION AND RESPONSE

The *habitat* consists of all the physical and chemical factors which in any way affect or modify the community. For land communities, a substratum in the form of soil with its attendant physiography is indispensable while the meteorological habitat factors, such as precipitation, temperature, relative humidity, *etc.*, constitute climate.

The basic soils of the oak and Douglas fir-hemlock communities are not significantly different. Following the system of classification in *Soils and Men*, the Yearbook of Agriculture for 1938, both are Gray-Brown Podzolic soils though the former is older and deeper than the latter. The physiography differs in that the oak community is on nearly level ground, with only a slight variation in elevation. The Douglas fir-hemlock community, however, is in a mountainous region which varies in elevation from a few hundred to 3500 feet or more with almost no level ground but numerous precipitous slopes.

To facilitate comparison of the climate of the two biotic communities, a climograph of each has been prepared by plotting the temperature against the precipitation for each month (Fig. 5). The climograph for the oak community is based on the average of conditions at Urbana, Illinois, for the 35-year period preceding 1937, while the one for the Douglas fir-hemlock community is based on the 4-year average from Saddle Mountain. In addition, a composite climograph representing the Oak-Hickory Association has been made by plotting the average conditions
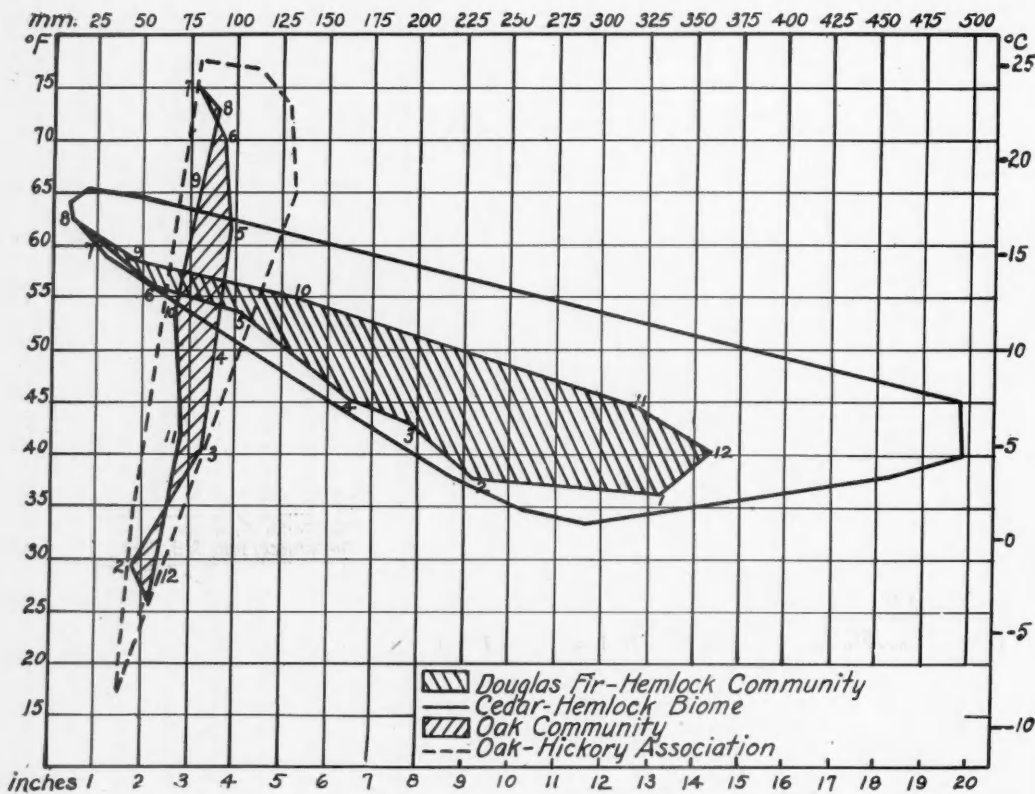
FIG. 5. Climographs of the Douglas fir-hemlock and oak communities showing their relation to one another and to the larger biotic units to which they belong. Temperature in degrees Fahrenheit and Centigrade is plotted against precipitation in inches and millimeters. See text for additional explanation.

given in the U. S. Weather Bureau reports for two localities in Missouri (Mexico and Lebanon), one in Illinois (Urbana), and one in southern Wisconsin (Madison). A similar composite based on the records from seven weather stations in Oregon and Washington (Tillamook, McKenzie Bridge, Coast Mountains (average of two locations), Saddle Mountain, Darrington, Forks, and Quinault) has been prepared for the Cedar-Hemlock Association. The resulting outlines are relatively regular in these composite climographs because only the outermost points have been connected.

The characteristic stability of the mean temperature for the Cedar-Hemlock Association—32 to 66 degrees, or a range of 34 degrees—and the great variability in precipitation per month—less than 0.5 to nearly 20 inches with the greatest amount falling during the winter months—are clearly shown. The mean temperature of the Douglas fir-hemlock community is slightly more stable and the precipitation is reduced in amount since the community studied is situated toward the southern end of the association.

The Oak-Hickory Association, on the other hand, is characterized by a much greater range in the mean monthly temperature—16 to 78 degrees, or 62 degrees—nearly twice the range for the Cedar-Hemlock

Association. Precipitation is much more uniform throughout the year—varying from about one and one-third to five and one-quarter inches per month. Again, the community under investigation shows slightly less variability than the larger unit.

Figures 6 and 7 give a more detailed comparison of the climate of the two communities. Precipitation, relative humidity, and temperature are shown graphically. One graph clearly emphasizes the fact that the least precipitation occurs in the Cedar-Hemlock Association during the summer seasons at the same time that precipitation is heaviest in the deciduous forest. From October to May, however, the rainfall is extremely heavy in the Douglas fir-hemlock community and rises above 12 inches per month in midwinter. The relative humidity graph shows that factor to be much less variable and constantly higher in the Douglas fir-hemlock community than in the oak community. The extreme variation in temperature in the deciduous woods between 1934 and 1937 was approximately 125 degrees, while the variation in the coniferous forest during that time was less than 80 degrees. The mean temperature in the deciduous forest falls about 10 degrees lower in the winter, rises about 10 degrees higher in the summer, and reaches its peak about a month earlier than the mean temperature for the Douglas fir-hemlock forest.
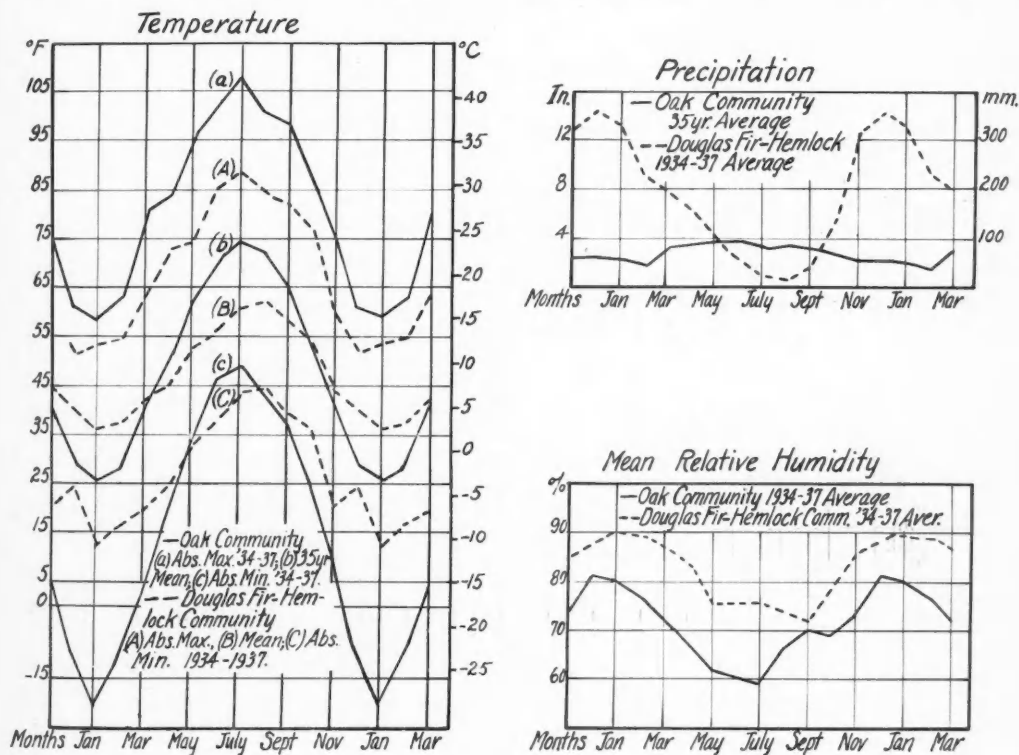
FIG. 6. Comparison of temperature, precipitation and mean relative humidity for the Douglas fir-hemlock and oak communities. See text.

Comparison of Temperatures
Douglas Fir-Hemlock Community

Shrub - Mean Max.
Mean, Mean Min. '34-37.
Tree - Mean '36-37
Soil - Mean '36-37

Oak Community

Shrub - Mean Max.
Mean, Mean Min. '34-37.
Soil - Mean '36-38.
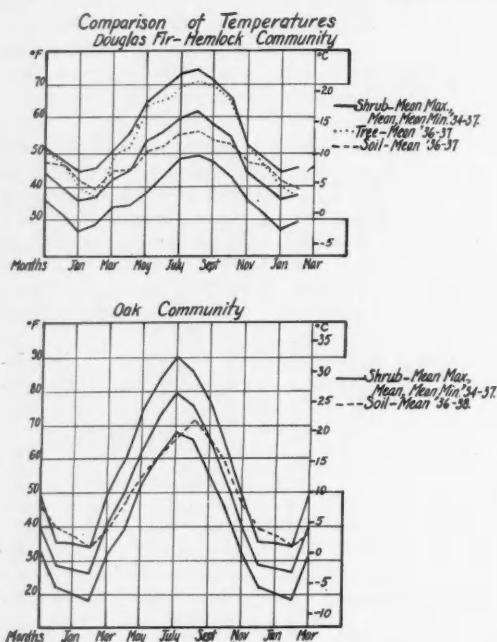
Fig. 7. Comparison of temperatures at various levels within the Douglas fir-hemlock and oak communities. Records were available for tree, shrub and soil strata of the former; shrub and soil strata of the latter. See text.

The habitats just discussed for the two communities act upon the attendant organisms in very characteristic ways, and the climax communities of the two localities are direct responses to the climates effective there. Neither of these two associations could have developed under the climate affecting the other. Heavy winter and low summer rainfall with slight variation in temperature throughout the year favor coniferous forests of Douglas fir, hemlock, cedar, and true firs, while relatively severe winters and reduced, but uniformly distributed, precipitation find expression in open deciduous woodlands of oak and other species with low moisture requirements. The additional associated plants and animals of the two communities are largely determined by the physical factors as modified by the reactions of these dominant species of trees.

REACTION

Reaction consists of the effects of organisms upon the habitat. A community accumulates or emphasizes influences that would otherwise be insignificant or transient; accordingly, the reactions of this larger biotic unit are greater than the sum of the reactions of the components as individuals. Many reactions are indirect results of coactions.

The reactions in the communities investigated are of two kinds: (a) those affecting the soil complex and (b) those modifying aerial factors.

Reactions Affecting Soil Complex. The numerous reactions affecting the soil complex are extremely diverse in nature. Some are primarily soil-forming and consist largely of the contribution of materials which will ultimately become soil. These are aided by reactions that prevent erosion of the soil and accumulated materials which are potential soil. Reactions which build soils and modify soil texture or structure are almost inseparable and are produced by both plants and animals.

Soil-forming reactions are composed of the accumulation of material, the resistance to its removal through rapid decomposition and erosion by wind and water, and the breaking down of the rock substratum into usable form through weathering processes.

In a forest community the trees contribute most of the material which becomes the humus layer of the soil. Logs, branches, leaves and needles all accumulate on the forest floor, while root systems add much ma-

Amount of Potential Soil Material from Plants in the Two Communities.
Estimates are for the two communities if left undisturbed for a long period of years.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
(a) From tree trunks Ave. number of trees per hectare	75 Douglas firs } 155 80 hemlocks	268
Ave. height (feet)	250 Douglas firs 150 hemlocks	85
Ave. diam. B.H. (ft.)	5.5 Douglas firs 4.0 hemlocks	3
Ave. longevity (years)	600 Douglas firs 400 hemlocks	250
Approx. vol. (per hectare) in 1000 years	1,000,000 cu. ft.	650,000 cu. ft.
(b) From needles and leaves	Small amount and continuous fall throughout year.	Large amount each autumn. Layer approximately 5 cm. deep in fall reduced to about 3 cm. by spring.
(c) From young trees and natural pruning	Lower branches shed as trees grow taller. Many young trees crowded out.	Similar but less pronounced.
(d) From shrubs	Largely evergreen; few leaves contributed throughout year.	Entire leaf growth each autumn.
(e) From herbs	Scattered in occurrence; contribute foliage of all and roots of annuals.	Uniformly dense growth; contribute foliage of all and roots of annuals.

terial under the surface. Herbs and shrubs, though smaller in size, also react to form soil. The rate at which this material accumulates varies, however, for the two communities studied. The chief differences are shown on the preceding page.

Like plants, animals react on the habitat to aid in accumulation of materials for soil formation through the deposition of their bodies. Some animals, however, may contribute several times their body weight in excreta during their life span; this is especially conspicuous in the feeding activities of Lepidoptera larvae. Recent studies on the millipedes and centipedes of a central Illinois forest by Ostendorf (1939) and Hanson (1941) show that these animals when at all abundant also are very important in this reaction, and some millipedes were observed to consume as much as one-twentieth of their body weight in leaves in one day's time while the excreta weighed well over one-half the weight of the food eaten. The excrement of all animals enriches the soil and increases its organic content. Material in this form is much more readily available as organic soil than are undecomposed trees, etc. The activities of saprozoic animals are important in influencing the rate of decomposition of dead vegetable matter, both underground and aboveground parts. Unfortunately, data are lacking for a quantitative comparison of saprozoans for the two communities.

A comparison of the invertebrate fauna of the two communities for the aestival and serotinal seasons reveals that the total number of individuals in the shrub, herb, and ground layers is nearly one and one-half times as large for the oak community as it is for the Douglas fir-hemlock community. Late in the summer the population total for the coniferous community is greatly increased by very small mites, which makes the difference in volume for the two communities even greater. Hence, a more accurate index may be obtained by comparing only insect populations. This shows approximately twice as many individuals for the oak community as for the other, and since the insects in the two communities appear to be about the same size, on the average, the volume of insects in the oak community is also about twice that of the Douglas fir-hemlock community.

The fauna of decomposing logs further complicates a comparison of the mass of invertebrates in the two communities. As mentioned previously, data for a quantitative comparison are not available. Logs are far more numerous in the coniferous forest than they are in the deciduous woods, but many of them are only slightly decayed and have a very small invertebrate population. The fauna of the more rotten logs is varied and abundant but the records secured indicate that the number of animals probably does not greatly exceed that in the logs in the oak community. This is a problem which evidently has had little attention and needs further study. Savely (1939) studied the ecological relations of certain animals in dead pine and oak logs, and while he examined both deciduous and coniferous logs, his study is of little value in comparing the numbers of individuals per unit area present in the two types of wood because he did not emphasize this type of quantitative work.

A comparison of bird population for the two communities further emphasizes the difference between the deciduous and coniferous forest communities. During the aestival-serotinal seasons an average of 20 birds exerted daily an effective influence in every hectare of the Douglas fir-hemlock community while the number for the oak community was approximately 35. These numbers are greater than the per hectare resident avian population for the communities since they include all birds which occurred in and affected any individual hectare. Though quantitative data for mammals are lacking, a significant difference in their reactions in the two communities is found in the absence from the oak community of the larger major influent animals. All act as soil formers through their excrement and the contribution of their bodies to the soil at death.

Accumulation of organic material on the forest floor is not the only soil-forming reaction of the trees and, to a minor degree, other plants. They retard decomposition of this organic material by protecting it from the effects of the climatic factors. They decrease water erosion by breaking the force of falling rain, by increasing receptivity of the soil to the rain—through the accumulated humus which they contribute in large degree, and by making possible more rapid penetration of the water into the soil—through root penetration. They prevent wind erosion by reducing the velocity of the moving air. Plant roots also bind the soil together and thus prevent its movement by wind. All of these reactions retard or prevent removal of the amassing organic soil-forming accumulation and favor increased volume and fertility of soil.

All of the protective reactions just discussed are more pronounced in the Douglas fir-hemlock forest than they are in the oak community because the trees in the former are nearly three times as high as they are in the latter, thus providing greater protection. The difference between the two communities in these respects is even greater during the late autumnal, hiemal, and prevernal seasons when the deciduous trees are without their leaves, and the material on the forest floor is exposed to nearly the full effect of temperature, rain, snow, wind, and sun. Thus, the organic accumulation of the forest floor decomposes and becomes organic soil more rapidly in the deciduous forest community than in the coniferous.

Weathering reactions, or conversion of rock into soil, constitute the third noteworthy group of reactions contributing to soil formation. Plants perform the preliminary activity in these processes through the mechanical force exerted by their growing roots and the action of the carbonic acid excreted by the roots. Since the extent of the root systems of the two groups of trees is not throughly known, comparison of these two factors is impossible.

Animals have a more important role in weathering reactions than is recognized frequently. The kinds of animals taking part in the conversion of rock and

Summary of Soil-forming Reactions of the Fauna of the Two Communities.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Invertebrates: (Based on M² collections)		
Shrub layer, average number of individuals	134	123
Herb layer, average number of individuals	270	199
Ground layer, average number of individuals	559	1251
Total............	963	1573
Insects—other than Apterygota: (Based on M² collections)		
Shrub layer, average number of individuals	74	117
Herb layer, average number of individuals	257	187
Ground layer, average number of individuals	134	519
Total............	465	822
Total weight or volume of invertebrate bodies	About one-half that of oak community.	About twice that of Douglas-fir hemlock community.
Leaf-eating excrement formers (Lepidoptera larvae, Hemiptera, Homoptera, *etc.*)	Very few. Aphids only ones ever common.	Many individuals and species.
Humus formers: Millipedes and centipedes	Many. Approximately five times number in oak community.	Fairly numerous.
Collembola	Common. Probably about as numerous as in oak community.	Common. Probably about as numerous as in Douglas fir-hemlock community.
Enchytraeidae	Common. Probably about as numerous as in oak community.	Common. Probably about as numerous as in Douglas fir-hemlock community.
Earthworms (Lumbricidae) Log fauna:	Common and large. Possibly silghtly more numerous than in oak community.	Rare and small. Possibly slightly less numerous than in Douglas fir-hemlock community.
Birds: excrement, bodies, *etc.*	20 individuals active per hectare, approximately.	35 individuals active per hectare, approximately.
Mammals: excrement, dead bodies, *etc.*		
A. Small	Common.	More numerous than in Douglas fir-hemlock community.
B. Large	Present—wide ranging.	Extirpated.

the reduction in size of particles of inorganic soil differ in a few striking respects in the two communities. These animals are shown in the following comparison.

Soil texture and structure reactions, as mentioned previously, are very closely akin to soil-forming reactions. The same processes, in fact, may have both results. Accumulation of humus changes the soil texture and structure as soon as the organic material becomes a part of the soil complex.

Incorporation of organic matter in the soil effects most of the important changes in the character of the soil. As pointed out previously, plants contribute by far the greater amount of this kind of material in the two communities studied though animals provide a small percentage of it (Jacot 1936). With the exception of the penetration of roots and underground stems into the soil—which subsequently die, decay, and are exfoliated—plants take little active part in the actual mixing of organic matter with mineral soil. Accordingly, the reactions which result in the mixing of the accumulated organic matter, plant and animal, with the inorganic soil and the formation of an organic layer in the soil complex are

Animals with Weathering Reactions.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Earthworms (Lumbricidae)	Common, large (adults 20 cm. or more in length), usually at least 50 cm. below soil surface in summer.	Rare, small.
Ants	Rare. Carpenter ant (*Camponotus herculeanus modoc* Whlr.) only species found; it frequents wood.	Abundant, often 50 to 100 per square meter. Penetrate deeply into soil.
Collembola	Numerous (36% of invertebrate population in ground layer).	Numerous (about 20% of invertebrate population in ground layer).
Mites	Fairly common.	Common.
Moles	Common.	Never observed.

due primarily to animals. Even the exfoliation of the roots and other underground plant parts is very largely an animal reaction and is performed by micro-arthropods which eat out the punky material resulting from fungous growth and leave the bark as indigestible corky tubes. In this way the soil is penetrated by a complex of ramifying tubes which enormously increase rain water percolation, aeration, and fertility, for the animals leave the empty rootlets lined with their droppings (Jacot 1936). Since details regarding the root systems for the two communities are lacking, a comparison of these reactions is impossible.

The mixing of humus with mineral soil which is brought about by animal activities permits a reutilization of the nutrients absorbed by previous generations, thus maintaining a balanced condition within the community. In addition, these activities increase the aeration of the soil and its capacity for water absorption and retention.

Every major group of animals in the two forest communities contains species with reactions which disturb the soil and participate in the mixing of the organic and mineral soils. Mammals, due to their greater size, probably are more important than any other group. Their digging activities are the most important in the process of transferring and mixing these materials.

The reactions of birds which effect incorporation of organic material in the mineral soil are secondary to those of the mammals and consist chiefly of surface scratching and dusting, only rarely penetrating to any considerable depth in the mineral soil. These are more important as fragmenting than as mixing reactions and are usually associated with feeding coactions. Only the birds present in the summer can be compared.

All invertebrates which frequent the ground layer react to change the texture and structure of the soil through mechanical impact of their bodies, tending to fragment larger particles, through the mixing which occurs as they penetrate below the organic layer, and through the increased porosity which their underground activities bring about. Saprozoans as reducers of humus add much to the soil in the form of readily available plant food. The animals which penetrate most deeply into the ground produce the greatest changes in the character of the soil. Since the deciduous forest has the larger soil invertebrate population during the summer seasons these reactions are more pronounced in it. During the late autumnal, hiemal, and prevernal seasons when most of the invertebrate life of the oak community is present in the ground layer, passing through the rigorous weather of the winter months, the contrast in the two communities is even greater. While the investigations reported here do not include the winter seasons for the Douglas fir-hemlock community, the

Animals with Soil-mixing Reactions.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Mammals		
Black bear	Abundant. Seen several times. Excavates yellow jacket nests, *etc.* Tears apart rotting stumps and logs, associated with food coaction.	Extirpated.
Mountain beaver	Common, especially in damper portions of community. Excavates extensive subterranean burrows.	Not present.
Chipmunk	Commonly seen. Excavates chamber in ground and lines this with leaves, *etc.* Stores food underground.	Possibly present but rare and not observed.
Spotted skunk	Seen, abundance not known. Probes into ground for insects, small mammals, *etc.* (Bailey, 1936).	Not present.
Mole	Common. Pushes mineral soil out onto surface of humus.	Never observed.
Creeping mouse	Common. Tunnels beneath soil surface are often mistaken for mole burrows.	Not present.
Red-backed mouse	Several caught. May burrow into humus or beneath. Some caught beside such burrows.	Not present.
Short-tailed shrew	Not present.	Common. Tunnels beneath softer soil surface and in humus layer.
Pine mouse	Not present.	Occurs. Not abundant though several caught. Reputed to center activities in mineral soil to depth of 18 inches (Jacot, 1940).
Fox squirrel	Not present.	Abundant. Buries many nuts and later digs them up.
Birds	Four species frequent ground layer. Grouse, varied and russet-backed thrushes, and winter wren. Places where grouse have been scratching have been seen. Other species have been observed on the ground.	Eight species frequent ground layer. Oven-bird, Kentucky warbler, wood thrush, cardinal, towhee, bob-white, mourning dove, brown thrasher. Bobwhite scratching activities have been observed. Robins overturn the leaves (Rice, 1946).
Invertebrates		
Earthworms	Common. Importance indicated previously.	Rare
Ants	Not present for this reaction.	Very abundant and important (discussed previously).
Myriapoda	15% of invertebrate population of ground layer.	2% of invertebrate population of ground layer.
Total number per M² aestival-serotinal seasons, ground layer	963	1573

Animals with Conspicuous Trampling Reactions.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Deer	Well-defined trails and "beds" conspicuous all over Saddle Mountain.	Extirpated.
Rabbit	Varying hare occurs. Trails fairly commonly seen especially in dense shrubby and herbaceous vegetation.	Cottontail occurs. Numerous runways observed.

writer's observations there have been that that community has no mass movement of invertebrates into the ground comparable with the hibernation of the animals in the oak community.

Another reaction which changes the character of the soil is the trampling of deer and other animals which follow definite routes in pursuance of their activities. Trampling reacts to destroy surface vegetation and compact the soil beneath, decreasing the absorptive capacity and aeration of the soil and favoring erosion. This trampling reaction is much more conspicuous in the Douglas fir-hemlock community than in the oak community because the large ungulates have been extirpated from the latter.

Reactions Modifying Aerial Factors. Light. The most readily observed reaction of the biota of a forest community upon the aerial factors is the reduction in light intensity. This is produced almost solely by the vegetation and principally by the trees which are much taller than the rest of the plants and thus dominate the community. The reduction in light intensity is brought about by reflection and absorption by the leaves of the plants and interception by their branches and trunks.

Comparison of Light Intensity in the Douglas Fir-Hemlock Community and the Oak Community.

A. Douglas fir-hemlock community—Weston Illuminometer readings in foot candles—2:15 to 2:50 P. M., June 25, 1937.

	Foot Candles
Opening in canopy	
Direct sun—humus surface	10,000 +
At edge of opening—shrub surface	8,500
Through low hemlock branches—shrub surface	625
Humus surface beneath shrubs	422
Humus surface beneath low hemlocks and shrubs	73
Shade of canopy	
Humus surface	100
Shade of trunk of large hemlock (6 to 10 feet from base)	73
Heavy canopy shade on shrub surface	55
Humus surface beneath shrubs	25

B. Oak community—Weston Illuminometer readings in foot candles —3:20 to 3:40 P. M., May 25, 1941.

Direct sun north of woods	9,000
Opening in canopy	
Herb level—in sun	6,060
Shrub surface	4,500
Beneath herbs	500
Ground surface	1,000
Shade of canopy	
Shrub surface	100
Herb surface	80
Ground surface	58
Shade of tree trunk—8 feet from base	
Shrub height	90
Ground surface	58

This reaction was not consistently measured for either community. However, on one clear June day, readings were obtained in foot candles by means of a Weston Illuminometer in the coniferous forest. The results are shown below. It should be noted that the vegetation reduced the light from over 10,000 foot candles in the open to approximately 25 foot candles beneath the shrubs in the shade of the forest canopy. A single record has been obtained for the oak community—May 25, 1941. The results, though not as extreme as those for the coniferous forest, are similar in nature and show that the foliage produces a marked reduction in light intensity.

The phenomenon of leaf fall in the deciduous forest with the resulting exposure of the forest floor to nearly full light intensity during the winter seasons should be recalled. However, in the coniferous forest during that time light conditions similar to those described previously for the Douglas fir-hemlock community still prevail and are modified only by lower intensity due to the high proportion of cloudy and rainy days during those seasons.

Precipitation. The trees of the Douglas fir-hemlock community are of sufficient height to intercept fog which condenses on the foilage of the canopy and thus materially increases the amount of precipitation. A comparison of the precipitation records for the two rain gauges—one beneath the forest canopy, the other under an opening—showed the amount of precipitation to be increased from about three-quarters of an inch additional to more than two additional inches each month from October through May.

A similar reaction may take place in the deciduous forest in the process of formation of dew though no attempt has been made to study it in this investigation.

Wind, Temperature, and Humidity. The tall trees, heavy canopy, and density of plant growth in a forest community react to decrease wind velocity through interception and, to a less extent, deflection. The vegetation also modifies the extremes of temperature by reflection and interception, lowering the maximum; the living and dead plant cover serves as a thermal blanket to retain the heat that has entered, thus raising the minimum. The decreased wind velocity also favors these modified temperature extremes. The thermal blanketing effect is shown graphically for both communities in Fig. 7. In both instances the temperature of the soil shows far less variation than does the temperature of the shrub level. Temperature readings for the tree layer were not obtained in the oak community, but the mean temperature for the tree layer (only 138 feet above the ground) of the Doug-

las fir-hemlock community varied much more than the mean shrub temperature.

Humidity is dependent upon the rate of transpiration and evaporation. Since transpiration is relatively high in forests and the reduction in air movement retards evaporation, relative humidity is higher in forests than outside of them.

Not all of these reactions have been studied quantitatively for the two communities in question. However, in a comparison of a coniferous forest in Maine with an Illinois deciduous forest, Blake (1926) found that the differences in physical conditions in the corresponding layers of the two communities were insignificant, and it is probable that this is true also for the oak and Douglas fir-hemlock communities during the summer seasons. The oak community varies within itself with respect to these reactions in the summer and winter seasons. The Douglas fir-hemlock community, on the other hand, is quite stable; accordingly, the two communities must differ greatly during the winter seasons. Since these reactions are largely dependent upon the height of the trees, and the coniferous trees are much taller than the deciduous, it also seems apparent that these reactions should be greater in the Douglas fir-hemlock community. This group of reactions is very important to the previously discussed soil accumulation reactions in retarding rate of decomposition of organic matter.

Though the reactions of the two biotic communities differ in detail and amount they are similar in effect. All of them help to bring about and maintain conditions which favor their respective climaxes.

COACTION

Coaction consists of the influence of organisms upon one another. This type of interaction is concerned with the actual control of the community by the dominant species and the basic shelter and food relations of organisms. From these fundamental interrelationships numerous and diverse secondary coactions of more specific and limited character arise. Many coactions involve reactions as well. While reactions result principally from plant presence and activity, coactions are largely expressions of animal activities and are very important in producing dynamic balance and unity in land communities.

Organisms are involved in coactions in two ways.

They may be the active, initiating or directing organisms known as the *coactors*, or they may be the passive or receiving organisms known as the *coactees*.

The following account will consider only the more common or conspicuous of the coactions in the two communities investigated. Three classes of coactions will be discussed: (a) competition and cooperation among the plant species, (b) shelter and housing coactions, and (c) food coactions.

Plant Competition and Cooperation. The processes of competition and cooperation as illustrated by plants in land communities are based on reactions by means of which the community modifies the habitat in some degree to its advantage. They are largely indirect and passive in their expression. In forest communities, water and light are the primary factors concerned. In the development of layers in the community, competition is the process involved. After dominance is once established, cooperation functions.

In both communities the thermal blanketing effect of the trees is of importance to both the flora and fauna in reducing the rate and amount of evaporation and the extremes of temperature to which they would otherwise be subjected.

Shelter and Housing Coactions. In the coactions of this group, animals are the coactors and plants the coactees. Plant cover is very important for animal resting and nesting sites. This fact is well known to students of vertebrate animals though it is not so obvious for many invertebrates. The summary which follows gives the more readily observed coactions of this kind.

Food Coactions. These interrelationships are of such complexity and importance in community dynamics that detailed diagrams have been made by some investigators, especially for deciduous forest communities (Bird 1930, Twomey 1937, Rice 1946). Food coactions in the communities studied are of two kinds (1) those in which animals are the coactor and plants the coactees, and (2) those in which animals are both coactors and coactees.

A consideration of the coactions of the plants and animals in a community shows that these interrelationships can be very diverse and complex and that the whole dynamic equilibrium of the unit depends upon the proper balance of the associated organisms within it (see also Tables 1-4).

Evidences of Dominance of Trees in the Two Communities.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Reduction of light by dense canopy	Approximately 155 very large trees per hectare.	About 270 much smaller trees per hectare.
Seedlings	Young Douglas firs (subclimax trees) cannot survive in dense shade. Young hemlocks grow well (climax trees).	Climax seedlings grow well.
Shrubs	Species of low light requirements. Most of them are evergreen also.	Species of low light requirements. Mostly deciduous because not protected in winter when leaves of trees have been shed.
Herbs	Species of low light requirement. Scattered in occurrence.	Species of low light requirement. Abundant and regular in distribution.

Comparison of the Shelter and Housing Coactions of the Animals in the Two Communities.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
In Trees **Mammals** Tree squirrel	Douglas's squirrels have been seen and heard occasionally. Nest either in hollow trees or in leaf, twig and moss nests among branches of conifers.	Fox squirrels make large leaf nests or platforms in trees in summer time. Many of these are present in the community studied. Have permanent nests in cavities in tree trunks.
Flying squirrel	Very probably occur though none have been observed. Habits similar to eastern species.	Permanent nests in tree cavities but reputed to use old fox squirrel leaf nests and occasionally make their own. Species fairly common though never seen except when trapped.
Opossum	Not present.	Probably present though not observed. Is said to hide away in tree trunks during day time.
Bats	Several seen. Number not known. Probably occur in trees and beneath loose bark.	Abundance not known. Never seen.
Birds	At least 3/4 of the bird population nests in the canopy, in cavities in the tree trunks, or in the young hemlock layer. This consists of about 20 species, all but 3 of which are permanent residents.	About 2/3 of the bird population nests in canopy, cavities, and seedlings. This comprises about 20 species, approximately 10 of which are permanent residents.
	Use chiefly dead plant material for nest construction.	Same.
In Shrubs **Birds**	Three or four species may nest here occasionally though usually in low trees. No nests have been observed. Chiefly permanent residents.	Four or five species may nest in this layer, though few nest were seen. Most of these birds are summer residents only.
In Ground Layer **Mammals** Rabbit	Snowshoe hare is reputed to nest on ground in dense growth of shrubby plants. No nests were found.	Cottontail excavates a chamber beneath ground surface usually. None was observed in the community.
Cougar, bear, bobcat, mink, weasel, spotted skunk, woodrat	Find shelter under accumulations of decaying logs and branches.	Weasel only one now present in this community.
White-footed mouse	Most abundant small mammal in community. Lives in and under decaying wood and beneath bases of trees.	Most abundant small mammal in community. Nests in much the same kind of locations as in the coniferous forest.
Subterranean species of mammals were discussed previously in section on reaction.		
Birds	Grouse and winter wren nest on ground though no nests were located.	Oven-bird, Kentucky warbler, bob-white, and mourning dove nest on ground.
Invertebrates	Shelter coactions usually associated with feeding coactions.	Usually associated with feeding coactions except when they hibernate beneath leaves and decaying wood in the winter seasons.

See also Tables 1 to 4.

ASPECTION

Aspection is the seasonal rhythm of appearance, growth and reproduction exhibited by the plants and animals in a community.

Several investigators who have made bio-ecological studies have described the seasons observed in their respective communities (Weese 1924, Smith 1928, Shackleford 1929, Twomey 1937, Jones 1946; *et al.*). The classification of seasons used in this paper is based on the oak community study and is in general agreement with the statements of these workers.

Season	Average Dates
Hiemal	Nov. 1 to March 1
Prevernal	March 1 to April 15
Vernal	April 15 to June 1
Aestival	June 1 to July 15
Serotinal	July 15 to Sept. 1
Autumnal	Sept. 1 to Nov. 1

Although the investigation presented here for the Douglas fir-hemlock community was restricted to the months of June, July, and August, the writer has visited this community in every month of the year and believes that the seasonal classification given for the deciduous forest is inadequate for the coniferous forest. This belief has been substantiated by the findings of Macnab (1944). On account of the limited observations reported in the present study, the comparison which follows is very incomplete for the Douglas fir-hemlock community and is arranged according to the seasonal chart for the oak community.

A striking example of aspection in the oak community was observed in the migration of robins (Fig. 8). In the spring of 1938, and again in 1939, the floodplain of the Sangamon River was inundated at the time when these birds were migrating northward. In 1939 a period of cold weather set in also after the robins had started their northward migration. This combination of factors resulted in an extremely large aggregation of the species in the oak community. When the woods was visited on March 18, 1939, approximately 500 of these birds were observed. The leaf litter looked as though it had been stirred with a rake, the activity of the robins had been so great

Another visit was made to the community two weeks later (April 1) and about 300 robins were still present. This abnormally large bird population through a period of more than two weeks must have had a great effect upon the invertebrate population. There was a decided drop in the number of invertebrates in the vernal season of that year, and this may very well have been due at least partially to the presence of the robins. The number of animals taken in the collections from the ground layer showed a marked drop at that time. It is interesting to note that the robins, which are chiefly ground feeders, migrate northward earlier than most of the other forest species, many of which are active in the trees. This earlier migration of the robins coincides rather closely with the period of greatest activity of invertebrates in the ground layer—during the prevernal season—when the hibernating forms are abundant in the humus and upper part of the soil just before they move up into the plant layers (Fig. 9).

In 1938, as mentioned earlier, the robins also were present at a time when they were restricted to the uplands because the floodplain was under water. That year they were numerous when the community

was visited on April 10, but the number present (100) does not approach the figures for the following year.

Robins are present again in fair numbers during the fall migration, but the lower community along the river is not flooded at that time and the migration of robins extends over a longer period of time. As a result not more than 50 individuals of the species have been observed in any one week.

TABLE 1. Coactions of Birds of the Douglas Fir-Hemlock Community.

Group: Prevalent (PR—permanent resident) or Seasonal (SR—summer resident).
Layers affected for food: T—tree, YH—young hemlock, S—shrub, H—herb, G—ground; parentheses indicate incidental effect.

Species	Group	Diet	Layers Affected for Food
Major Influents			
Sharp-shinned hawk, *Accipiter velox* (Wilson)	PR	Carnivorous	T(YH,S,H,G)
Cooper's Hawk, *A. cooperi* (Bonaparte)	PR	Carnivorous	T(YH,S,H,G)
Red-tailed Hawk, *Buteo borealis* (Gmelin)	PR	Carnivorous	G
Sooty grouse, *Dendragapus fuliginosus* (Ridgway)	PR	Omnivorous	YH,S,H,G
Band-tailed Pigeon, *Columba fasciata* Say	SR	Seeds & Fruits	T,S
Screech Owl, *Otus asio* (Linnaeus)	PR	Carnivorous	G(T,YH,S,H)
Horned Owl, *Bubo virginianus* (Gmelin)	PR	Carnivorous	G(T,YH,S,H)
Pygmy Owl, *Glaucidium gnoma* Wagler	PR	Carnivorous	YH,S,H,G
Pileated Woodpecker, *Ceophloeus pileatus* (Linnaeus)	PR	Insectivorous	T
Raven, *Corvus corax* Linnaeus	PR	Omnivorous	T
Minor Influents			
Hairy Woodpecker, *Dryobates villosus* (Linnaeus)	PR	Insectivorous	T
Western Wood Pewee, *Myiochanes richardsoni* (Swainson)	SR	Insectivorous	T
Oregon Jay, *Perisoreus obscurus* Ridgway	PR	Omnivorous	T,YH,S,H,G
Steller's Jay, *Cyanocitta stelleri* (Gmelin)	PR	Omnivorous	T,YH,S,H,G
Chestnut-backed Chickadee, *Penthestes rufescens* (Townsend)	PR	Insectivorous	T,YH,S
Red-breasted Nuthatch, *Sitta canadensis* Linnaeus	PR	Insectivorous	T
Brown Creeper, *Certhia familiaris* Linnaeus	PR	Insectivorous	T
Winter Wren, *Nannus hiemalis* (Vieillot)	PR	Insectivorous	G
Varied Thrush, *Izoreus naevius* (Gmelin)	PR	Omnivorous	G,YH,S,H
Russet-backed Thrush, *Hylocichla ustulata* (Nuttall)	SR	Omnivorous	G,YH,S,H
Golden-crowned Kinglet, *Regulus satrapa* Lichtenstein	PR	Insectivorous	YH,S
Hermit Warbler, *Dendroica occidentalis* (Townsend)	SR	Insectivorous	T
Pine Siskin, *Spinus pinus* (Wilson)	PR	Conifer Seeds	T
Red Crossbill, *Loxia curvirostra* Linnaeus	PR	Conifer Seeds	T

TABLE 2. Coactions of Birds of the Oak Community.

Group: Prevalent (PR—permanent resident) or Seasonal (WR—winter resident, SR—summer resident, AV—annual visitant, OV—occasional visitant).
Layers affected for food: T—tree, S—shrub, H—Herb, G—ground; parentheses indicate incidental effect.
Migrants: Warblers, flycatchers, and vireos have been observed busily searching for and obtaining insects, larvae, etc.
Occasional Visitants: Birds from the surrounding fields have been noted occasionally.

Species	Group	Diet	Layers Affected for Food
Major Influent			
Red-shouldered Hawk, *Buteo lineatus* (Gmelin)	PR	Carnivorous	G
Screech Owl, *Otus asio* (Linnaeus)	PR	Carnivorous	G
Minor Influent			
Bob-white, *Colinus virginianus* (Linnaeus)	PR	Insects, Seeds	G
Mourning Dove, *Zenaidura macroura* (Linnaeus)	SR	Grains, Insects	G
Yellow-billed Cuckoo, *Coccyzus americanus* (Linnaeus)	SR	Insectivorous	T,S
Ruby-throated Hummingbird, *Archilochus colubris* (Linnaeus)	SR	Nectar	S,H
Yellow-shafted Flicker, *Colaptes auratus* (Linnaeus)	SR	Omnivorous	T,G
Red-bellied Woodpecker, *Centurus carolinus* (Linnaeus)	PR	Omnivorous	T,G
Red-headed Woodpecker, *Melanerpes erythrocephalus* (Linnaeus)	SR	Omnivorous	T,G
Hairy Woodpecker, *Dryobates villosus* (Linnaeus)	PR	Insectivorous	T
Downy Woodpecker, *D. pubescens* (Linnaeus)	PR	Insectivorous	T
Crested Flycatcher, *Myiarchus crinitus* (Linnaeus)	SR	Insectivorous	T
Eastern Wood Pewee, *Myiochanes virens* (Linnaeus)	SR	Insectivorous	T
Blue Jay, *Cyanocitta cristata* (Linnaeus)	PR	Omnivorous	T
Crow, *Corvus brachyrhynchos* Brehm	PR	Omnivorous	G
Black-capped Chickadee, *Penthestes atricapillus* (Linnaeus)	PR	Insectivorous	T,S
Tufted Titmouse, *Baeolophus bicolor* (Linnaeus)	PR	Insectivorous	T
White-breasted Nuthatch, *Sitta carolinensis* Latham	PR	Insectivorous	T
Brown Creeper, *Certhia familiaris* Linnaeus	WR	Insectivorous	T
House Wren, *Troglodytes aedon* Vieillot	SR	Insectivorous	S
Brown Thrasher, *Toxostoma rufum* (Linnaeus)	SR	Insects, Fruits, Grain	S,G
Wood Thrush, *Hylocichla mustelina* (Gmelin)	SR	Insectivorous	S,T
Golden-crowned Kinglet, *Regulus satrapa* Lichtenstein	WR	Insectivorous	S,T
Yellow-throated Vireo, *Vireo flavifrons* Vieillot	SR	Insectivorous	T
Red-eyed Vireo, *V. olivaceus* (Linnaeus)	SR	Insectivorous	S,T
Oven-bird, *Seiurus aurocapillus* (Linnaeus)	SR	Insectivorous	G,(H)
Kentucky Warbler, *Oporornis formosus* (Wilson)	SR	Insectivorous	G,H
Scarlet Tanager, *Piranga erythromelas* Vieillot	SR	Insects, Seeds, Berries	T
Cardinal, *Richmondena cardinalis* (Linnaeus)	PR	Seeds, Fruit, Insects	S,G
Indigo Bunting, *Passerina cyanea* (Linnaeus)	SR	Seeds, Berries, Insects	S,(G)
Red-eyed Towhee, *Pipilo erythrophthalmus* (Linnaeus)	SR	Seeds, Fruit, Insects	G
Slate-colored Junco, *Junco hyemalis* (Linnaeus)	WR	Seeds, Insects	G
Migrants	AV	Insects chiefly	All
Occasional Visitants	OV	All types	All

TABLE 3. Coactions of Mammals of the Douglas Fir-Hemlock Community.

Group: Prevalent (P—active the year-round) or Seasonal (S—hibernates in winter).
Layers: T—tree, YH—young hemlock, S—shrub, H—herb, G—ground. The ones in parentheses are incidental or indirect.

Species	Group	Diet	Layers Affected for Food
Major Influents			
Col. Black-tailed Deer, *Odocoileus c. columbianus* (Richardson)	P	Browse	S,H,G,(YH)
Black Bear, *Euarctos americanus altifrontalis* (Elliot)	S	Omnivorous	S,H,G
Ore. Cougar, *Felis concolor oregonensis* Rafinesque	P	Carnivorous	G,S,H,(YH)
Ore. Bobcat, *Lynx rufus fasciatus* Rafinesque	P	Carnivorous	G,S,H
Spotted Skunk, *Spilogale phenax latifrons* Merriam	P	Omnivorous	G
Western Mink, *Lutreola vison energumenos* (Bangs)	P	Carnivorous	G
Puget Sound Weasel, *Mustela cicognanii streatori* (Merriam)	P	Carnivorous	G
Pacific Mountain Beaver, *Aplodontia rufa pacifica* Merriam	P	Herbivorous	G,H,S
Snowshoe Hare, *Lepus americanus washingtonii* Baird	P	Herbivorous	S,H,YH,G
Minor Influents			
Douglas's Squirrel, *Sciurus douglasii douglasii* Bachman	P	Herbivorous	T,YH
Oregon Flying Squirrel, *Glaucomys sabrinus oregonensis* (Bachman)	P	Omnivorous	T
Bushy-tailed Wood Rat, *Neotoma cinerea fusca* True	P	Herbivorous	S,H,G
Townsend's Chipmunk, *Eutamias townsendii townsendi* (Bachman)	S	Omnivorous	G,S,H,(YH)
White-footed Mouse, *Peromyscus maniculatus rubidus* Osgood	P	Omnivorous	S,G,H
Oregon Creeping Mouse, *Microtus oregoni oregoni* (Bachman)	P	Herbivorous	G
Cal. Red-backed Mouse, *Clethrionomys californicus californicus* (Merriam)	P	Herbivorous	G
Little Big-eared Bat, *Myotis evotis evotis* (H. Allen)	S	Insectivorous	T(H,S,YH)
Coast Mole, *Scapanus orarius orarius* True	P	Insectivorous	G
Trowbridge's Shrew, *Sorex trowbridgii trowbridgii* Baird	P	Insectivorous	G

TABLE 4. Coactions of Mammals of the Oak Community.

Group: Prevalent (P—present the year-round) or Seasonal (S—hibernates in winter). The opossum may not hibernate in the true sense of the word but is inactive during the most severe weather.
Layers affected for food: T—tree, S—shrub, H—herb, G—ground. The ones in parentheses are incidental or indirect.

Species	Group	Diet	Layers affected for food
Major Influent			
Opossum, *Didelphis v. virginiana* Kerr	S	Omnivorous	G,T
N.Y.Weasel, *Mustela frenata noveboracensis* (Emmons)	P	Carnivorous	G,(S,H,T)
Fox Squirrel, *Sciurus niger rufiventer* Geoffroy	P	Herbs & Insects	T,(G,S)
Mearns Cottontail, *Sylvilagus floridanus mearnsii* (Allen) (Forest edge animal.)	P	Herbivorous	G,H,S
Minor Influent			
Flying Squirrel, *Glaucomys v. volans* (Linnaeus)	P	Herbs & Insects	T,(G,S)
Chipmunk, *Tamias striatus griseus* Mearns	S	Omnivorous	G,(H,S,T)
White-footed Mouse, *Peromyscus leucopus noveboracensis* (Fischer)	P	Herbs & Insects	G,(H,S)
Pine Mouse, *Pitymys pinetorum scalopsoides* (Audubon and Bachman)	P	Roots, tubers	G,(H,S,T)
Short-tailed Shrew, *Blarina brevicauda* (Say)	P	Insectivorous	G
Little Shrew, *Cryptotis parva* (Say)	P	Insectivorous	G

Figures 9 and 10 give a graphic presentation of the seasonal distribution of the insect population (exclusive of Apterygota) for the two communities. It should be noted that the peak of insect population occurs in the autumnal season in the oak community just before hibernation begins, when the adult population has not yet died off and many immature individuals are present. Figure 10 is based on data obtained from the research investigation of Dr. James A. Macnab in the Oregon Coast Range Mountains.

Comparison of Food Coactions in the Two Communities.

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Animals with Plant Coactees 1. Grazing or browsing coactions. (All coactions involving consumption of leaves, needles, and buds of plants as food.)		
Deer	Abundant. Feed on vegetation throughout year; eat herbs and shrubs primarily since ferns and salal are present the year round.	Extirpated.
Rabbit	Snowshoe hares are common. Food similar to that of deer.	Cottontail common, especially around forest edge during milder seasons, moving farther into woods in winter.
Mountain beaver	Common. Feed on almost any kind of vegetation available, particularly ferns and young shrubby growth.	Not present.
Bushy-tailed wood rat	Some seen; abundance not known. Reputed to feed largely on vegetation, laying away "hay" in nests.	Not present.
Chipmunk	Common. Probably browse to some extent.	May occur but not observed. Probably browse some.
Creeping mouse	Common. Probably browse to some extent.	Not present.
White-footed mouse	Abundant. Browse some.	Abundant. Browse.
Red-backed mouse	Several caught; feed on vegetation (Macnab and Dirks, 1941).	Not present.
Sooty grouse	Several seen. Feed chiefly on hemlock buds in winter (Gabrielson and Jewett, 1940).	Not present.
Leaf-eating beetles (Chrysomelidae)	Salal beetle (*Timarcha intricata* Hald.) and a few other species are common.	About 30 species are present, some of which are common.
Lepidoptera	Pine butterfly (*Neophasia menapia* Feld.) larvae feed on Douglas fir needles (Keen, 1939). Green hemlock looper (*Nepytia phantasmaria* Stkr.) feeds on hemlock and Douglas fir needles (Doane, *et al.*, 1936). Salal leafmining Microlepidoptera larvae common on salal leaves. Several other unidentified browsers have been observed though their activities were not extensive.	Defoliating activities of several species have been observed. Pyraustidae larvae are common on leaves of young linden trees.

Comparison of Food Coactions in the Two Communities. *(Continued)*

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Gastropoda	The large green and black-spotted slugs (*Ariolimax columbianus* (Gould) and *A. c. maculatus* Cockerell) have been seen feeding on ferns and other plants of the shrub layer.	Young snails, particularly *Mesodon thyroidus* (Say), often feed on herbs and shrubs in summer.
2. Sucking coactions. Homoptera (suck juices from leaves and stems in both communities)		
Aphids	33% of herb invertebrates, 14% of shrub. Very abundant on salal and herbs in aestival and early serotinal seasons.	About 29% of herb invertebrates, 28% of shrub (aestival and serotinal seasons). Abundant on herbs, shrubs and young elm leaves.
Leafhoppers	Few species and individuals.	Extremely abundant; many species.
Treehoppers	Not present.	Few.
Fulgorids	Few.	Several species, two or three of which are fairly common.
Hemiptera (many suck plant juices)	Few species and individuals. Less than 1% of invertebrate population of herb and shrub layers.	Fairly common, about 15% and 6% of the invertebrate population in shrub and herb layers, respectively. Many species.
3. Seed and fruit eating coactions.		
Black bear	Mother and two cubs seen eating huckleberries.	Extirpated.
Tree and flying squirrels	Though not observed in specific area studied Douglas's and flying squirrels commonly eat conifer seeds.	Large quantities of acorns eaten by fox and flying squirrels. Shells are commonly seen about bases of trees where there are nests.
Chipmunk	Several have been seen eating huckleberries. Probably also eat other fruits and seeds.	If present, probably eats seeds and fruits.
White-footed mouse and other mice	Reputed to eat seeds and fruits.	Same.
Shrew	Trowbridge's shrew eats Douglas fir seeds readily (Moore, 1940 and 1941).	Not known.
Sooty grouse	Have been seen working about salal bushes as though eating berries.	Not present.
Band-tailed pigeon	Largely a fruit and seed-eating species (Gabrielson and Jewett, 1940). Has been seen several times but never while feeding.	Not present.
Crossbills	Often observed. Eat conifer seeds.	Not present.
Omnivorous birds	About 4 species probably eat seeds and fruit in season.	About 10 species feed partially on seeds and fruits.
4. Other plant feeding coactions.		
Formation of galls	Gall midges (Cecidomyidae) are common in shelter of young hemlock branches. Specific effects of these have not been noted. A few Cynipidae (gall-making Hymenoptera) occur.	Three species of psyllids (*Pachypsylla celtidisvesiculum* Crawford, *P. c.-mamma* Riley, and *P. c.-gemma* Riley) occur on hackberry; galls are very conspicuous. A few cynipid gall-makers have been collected which form oak galls.
Cambium eaters	Several species of Scolytidae (bark beetles) are present. Some are fairly numerous; they feed principally on dead trees or logs.	No Scolytidae observed.
Root eaters	Several weevils and click beetles, the larvae of which have these habits, have been collected.	Pine mice feed extensively on roots and underground tubers (Hamilton, 1938).
Flower frequenters	Small-headed fly (*Eulonchus sapphirinus* O.S.) abundant on Clintonia flowers late in June. Bumblebees have been seen on flowers.	One or two pair of ruby-throated humming birds usually nest in community each summer. Several species of Cantharidae are common on blossoms. Bumblebees are observed rather often.
Plant scavengers Rove beetles	Abundant.	Abundant.
Collembola	Abundant.	Abundant.
Large silverfish (Thysanura)	Occur occasionally.	Not observed.
Millipedes	Very common.	Common.
Beetles feeding on rotten wood	Species from five families commonly feed on rotten wood: Tenebrionidae, Elateridae, Lucanidae, Cerambycidae, and Scolytidae.	Same families represented as in coniferous wood except Scolytidae which are not present.
Psocids	Several species are fairly common on tree trunks and young hemlocks.	One species occurs occasionally. Not common.
Fungus feeders	Small grey slug (*Prophysaon* sp.) has been seen feeding on fungus several times. One or more species of Collembola are abundant at times on slime mold. Numerous species of fungus gnats (Mycetophilidae) are abundant.	Several species of fungus gnats (Mycetophilidae) occur though they are not abundant.

Animals with Animal Coactees
1. Vertebrate coactees.

Comparison of Food Coactions in the Two Communities. *(Continued)*

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Cougar, bob-cat, mink, weasel, great horned owl, red-tailed hawk, Cooper's hawk, sharp-shinned hawk, pygmy owl	All are active predators on mammals and birds ranging in size from deer to shrews and kinglets. (Bailey, 1936; Bent, 1937; and personal observation.)	Weasel and screech owl are the only ones of the group which occur. They prey on small mammals and birds.
Red-shouldered hawk	Not present.	Reputedly preys on mice, *etc.*
Shrew	Trowbridge's shrew is fairly common; possibly feeds on mice to some extent.	Short-tailed and little shrews both present. Both are at least partially carnivorous. Trapping results indicate little shrew may be highly so.
Black bear, Spotted skunk	Omnivorous; hence probably partly carnivorous.	Do not occur here.
Opossum	Not present.	Omnivorous; hence probably somewhat carnivorous
Deer flies (Tabanidae) and blood-sucking flies (Leptidae)	Common.	Few.
Mosquitoes	Common.	Common.
2. Invertebrate coactees.		
Black bear	Have seen excavated yellow-jackets' nests and logs which have been torn up by bears.	Extirpated.
Spotted skunk, Mole	Reputed to feed largely on insects (Bailey, 1936).	Not present.
Tree squirrel, flying squirrel, opossum, mice, shrews	All but opossum occur. All are reputed to eat insects.	All occur. Insects comprise much of diet (Hamilton and Cook, 1940; Nelson, 1930; *et al.*).
Weasel	Occurs in this community, but this coaction not verified.	Insects and earthworms may be included in their dietary in the winter (Hamilton, 1937).
Chipmunk	Reputed to eat some insects.	May be present; reputed to eat insects.
Birds	9 insectivorous species; 6 omnivorous species which include insects in diet. Several of these have been seen feeding on insects (also Bent, 1939 and 1940).	14 insectivorous species; 12 omnivorous. Many of these have been seen feeding on insects and larvae (also Bent, 1939 and 1940).
Amphibia	American bell toad (*Ascaphus truei* Stejneger); three species of salamanders occur (*Dicamptodon ensatus* (Eschscholtz), *Ensatina eschscholtzii* (Gray) and *Plethodon vehiculum* (Cooper)). Feed on insects and other small invertebrates.	None observed.
Spiders and mites (most species are active predators)	31% of total invertebrate population for all layers in the community. Coaction observed on numerous occasions.	8% of total invertebrate population for all layers in community during aestival-serotinal seasons. Observation (and Jones, 1946).
Parasitic Hymenoptera	Numerous species and individuals.	Numerous species and individuals.
Ants (honey-dew coaction)	Not present.	Several species with numerous individuals care for aphids, *etc.*, for honey-dew (Smith, 1927).
Predatory beetles	Ground beetles (Carabidae) common. Large black ground beetle (*Scaphinotus angusticollis*) observed eating earthworms and snails.	Ground beetles and lady-bird beetles (Coccinellidae) common.
Neuroptera
Raphididae	Collected several times. Larvae are predaceous and feed on many insect larvae and eggs.	None observed.
Lacewings	Hemerobids collected several times. Not common. Larvae feed on aphids, mites, scale insects.	Chrysopids common. Larvae feed on aphids. Hemerobids occur occasionally.
Predatory Diptera	Larvae of *Syrphus opinator* eat aphids; *Eulonchus sapphirinus* larvae prey on spiders and their eggs (Essig, 1936). Others undoubtedly present.	Identifications are very incomplete and effects have not been observed.

ANNUATION

Annuation refers to the annual modification in presence and number of organisms by the climatic cycle.

Douglas Fir-Hemlock Community. Annual differences in presence and number of the biota are not discernible in the present consideration of the Douglas fir-hemlock community because quantitative collections were made regularly in all layers only during the last year of this study and the study was restricted to the summer months.

Oak Community. Only a few of the more obvious annual responses of the organisms in the oak community will be mentioned since the investigation extended only over a two-year period and the writer was absent during most of the summer of 1938, with

the result that few collections were obtained during that period.

The most striking manifestation of annuation has been discussed already—the difference in the number of robins visiting the community in the spring of the two years (Aspection and Fig. 8). Other evidences of annuation among the birds were not clearly defined for two reasons: first, the proximity of the floodplain forest and the tendency of the birds to go to it during severe weather in the winter, and second, an incomplete nesting census in the summer of 1938, rendering detailed comparison of the two years impossible.

The mammal population estimates also are considered too incomplete to be used in this connection.

An inspection of Figure 9 makes clear some of the differences in number and distribution of insects in

Summary of Biotic Evidences of Aspection in the Two Communities.

		DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
A.	Aestival Invertebrates	Steady increase in number of Arachnids (particularly mites and immature spiders) in all plant layers throughout summer. Steady decrease in abundance of Homoptera (chiefly aphids). Small-headed fly (*Eulonchus sapphirinus*) on Clintonia flowers late in June. Herb insects reach peak of abundance at end of season (Fig. 10).	No striking change in abundance of Arachnids. Homoptera increasing in numbers. Invertebrate population restricted to forest forms. Immature invertebrates present in fair numbers. Much invertebrate activity on herbs and shrubs.
	Amphibia	Apparently aestivate.	None observed.
	Birds	Some evidence of continued nesting. Some young birds seen.	Bird population limited to permanent and summer resident species. Nesting continued though past peak. Young birds observed, bringing permanent residents to population peak.
	Plants	All except the earliest herbs bloom during this season. Ripened fruits begin to appear.	Jewelweed is the distinctive herb of aestival and serotinal seasons. Earlier herbaceous vegetation gradually dies.
	Mammals	Generally active; young appearing.	Generally active; young appearing.
B.	Serotinal Invertebrates	Homopterous population drops to very low level. Arachnid population reaches peak above previous season. Shrub insects reach peak early in aspect (Fig. 10). Characteristic insects are yellow jacket (*Vespula vulgaris*) and biting mosquitoes (*Aedes* spp.)	Homoptera gradually increasing in numbers. Number of adult invertebrates beginning to drop; immature to increase. Gradual increase in total invertebrate population; continued activity on herbs and shrubs.
	Amphibia	Renew activity.	No observations.
	Birds	Little evidence of nesting. Young birds seen occasionally.	Nesting largely over. Young birds observed frequently. First fall migrants appear. Summer resident population begins decreasing.
	Plants	Last fruits ripened. Herbaceous vegetation withers and dies.	Jewelweed still the distinctive herb.
	Mammals	About the same as aestival.	About same as aestival.
C.	Autumnal Invertebrates	(*This community not studied in detail.*) No "inward" migration; little evidence of "downward" migration. Mycetophagus fauna abundant. Second peak of abundance of herb and shrub insects (Fig. 10).	Migration of crop and forest edge invertebrates into woods. Progressive downward migration of most invertebrates. Disappearance of adults of many species. Peak of invertebrate population (Fig. 9).
	Amphibia	Second peak of abundance.	None observed.
	Birds	Summer residents leave.	Peak of southward migration. Winter resident species appearing.
	Plants	Herbs gone. Leaf fall not conspicuous because deciduous trees and shrubs are very few in number. Old needles fall from coinfers. Fungi abundant.	White snake-root is the only common herb. Leaf fall beginning.
	Mammals	Generally active.	Squirrels frequently observed storing nuts.
D.	Hiemal Invertebrates	(*This community not studied in detail.*) Less abundant but no striking evidence of hibernation for group as a whole.	Mostly hibernating in soil or beneath leaves in humus layer.
	Birds	Summer resident species gone. Winter residents observed.	Summer resident species absent. Winter resident species present.
	Plants	Herbs gone, otherwise much the same as rest of year.	Trees and shrubs barren of leaves. Herbs have all died down. Heavy carpet of leaves covers forest floor.
	Mammals	Much the same as warmer seasons. Deer, cougar, bobcat, rabbit, and mice tracks seen. Bears hibernating.	Several species hibernating. Mice, shrew and squirrel tracks observed in snow.
E.	Prevernal Invertebrates	(*Not studied in detail.*) Pollen-feeding insects common, especially Staphylinid beetles on skunk cabbage. Peak of ground population of invertebrates (Fig. 10).	Several species of spiders become active in ground layer. Several species of invertebrates (namely, Hemiptera, Homoptera, Diptera, Coleoptera) begin upward migration.
	Amphibia	Become active.	None observed.
	Birds	Hummingbird first observed; other summer residents begin to appear.	Early migratory species appear. Winter resident species present in large numbers due to migratory movements of birds which have been farther south.
	Plants	Herb buds begin unfolding.	In herb layer, spring beauty, violets, toothwort, squirrel corn, and Dutchman's breeches appear. Leaf buds on trees and shrubs begin swelling and unfolding.
	Mammals	Bears active; chipmunks first seen; sporadic evidence of mole activity.	Evidence of greater activity.
F.	Vernal Invertebrates	(*Not studied in detail.*) Large black ground beetle appears (*Scaphinotus angusticollis*). Cantharidae and Muscid flies common.	Invertebrate population large, due to upward migration. Many species active in herbs and shrubs. Crop species move toward forest edge. Immature forms of some species appear from over-wintering eggs.

Summary of Biotic Evidence of Aspection in the Two Communities. *(Continued)*

	DOUGLAS FIR-HEMLOCK COMMUNITY	OAK COMMUNITY
Amphibia	Reach first peak of abundance.	None observed.
Birds	Summer resident birds definitely present. Nesting begins.	Northward bird migration reaches its peak and terminates toward close of this season. Winter resident species disappear. Many birds are nesting.
Plants	Herbaceous vegetation at peak.	Trillium, Jack-in-the-pulpit, Solomon's seal, false Solomon's seal, and mandrake are the common herbs which usher in the vernal season, forming an abundant herbage. Trees and shrubs finish leafing out.
Mammals	Generally active.	Generally active.
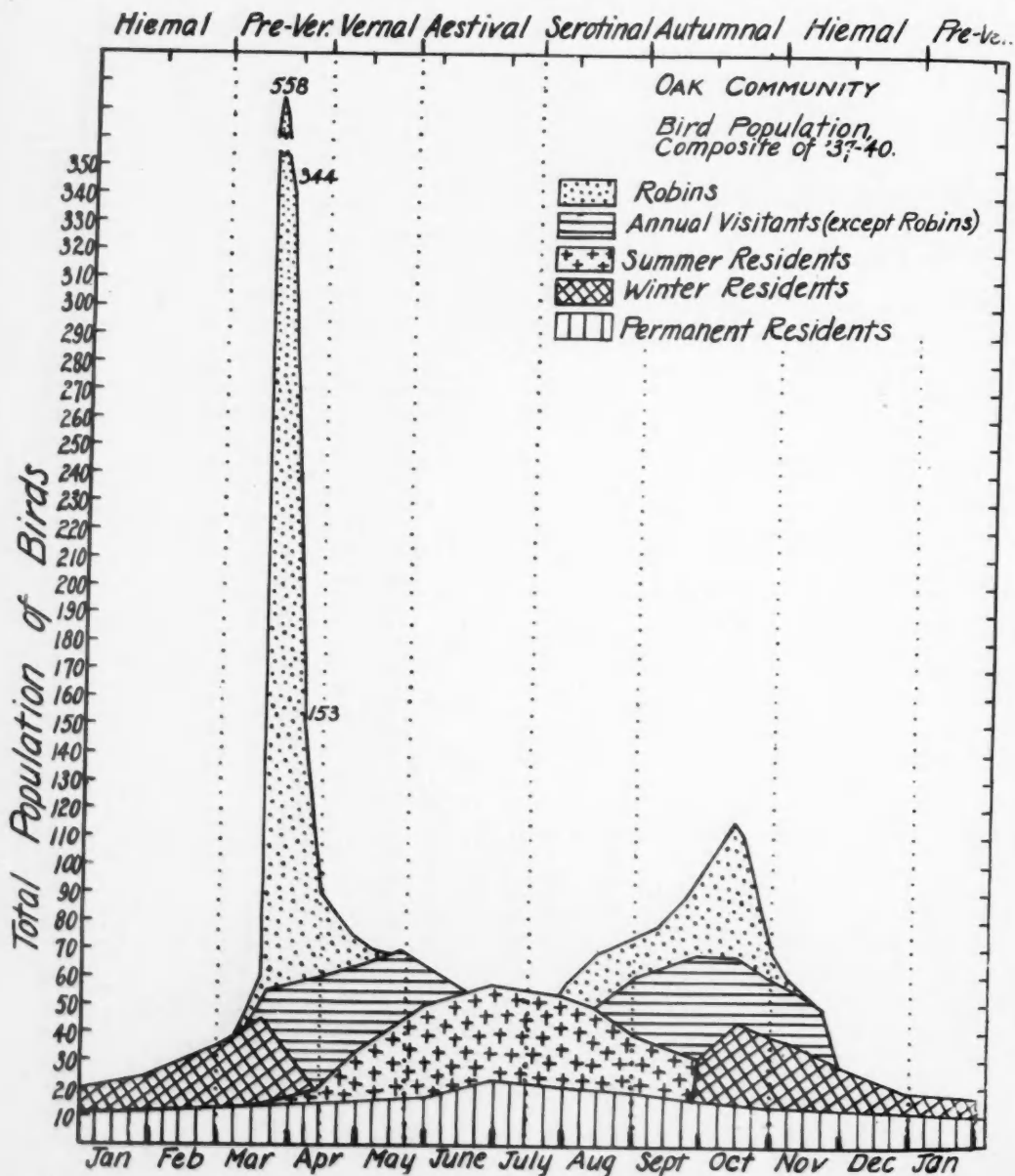
FIG. 8. Composite graph representing the total bird population in the oak community during the years 1937 through 1940. See text.

FIG. 9. Seasonal distribution of the insect population (exclusive of Apterygota) by strata in the oak community for 1938-1939. Population is expressed in terms of number of insects per square meter. See text.

the layer societies during the comparable seasons of the two years. The greatest difference occurred during the vernal seasons. This is believed to be at least partially correlated with the robin migration in the spring of 1939, for at that time the forest floor was literally alive with birds hunting insects in the leaf litter. With this one exception, the insect population was a little higher in 1938-39 than in the preceding year. This may be due to the fact that the preceding winter was somewhat milder, having a mean temperature which averaged 5 degrees higher through the months of November through January. However, February through April in 1938 averaged 6 degrees higher than that period for 1939. This low temperature in the spring of 1939 retarded the vernal season approximately two weeks (until about the first of May though the conventional dates are used in the graph) and was reflected both in the time of appearance of vegetation and end of hibernation of the invertebrate fauna.

SUMMARY

1. A comparison of the climatic conditions affecting the two communities shows that there is much greater precipitation and higher relative humidity in the Douglas fir-hemlock community, but the mean temperature is higher and more variable in the oak community.

2. The plants and animals in the two communities constitute ecologically equivalent groups. The list which follows indicates the more important taxonomic differences.

	Douglas fir-hemlock community	Oak community
A. DOMINANTS Trees	*Pseudotsuga taxifolia* *Tsuga heterophylla* *Abies nobilis, et al.* *Thuja plicata**	*Quercus alba* *Quercus borealis maxima* *Quercus velutina* *Carya ovata* *Carya cordiformis* *Juglans nigra* *Ulmus americana* *Ulmus fulva*
B. SUBDOMINANTS Shrubs	Deciduous *Vaccinium ovalifolium* *Vaccinium parvifolium* Evergreen *Berberis nervosa* *Gaultheria shallon* *Polystichum munitum*	Deciduous *Sambucus canadensis* *Euonymus atropurpureus* *Ribes* sp. *Crataegus* spp. *Pyrus* sp. *Symphoricarpos orbiculatus* *Viburnum* sp.
Herbs	*Achlys triphylla* *Oxalis oregona* *Juncoides parviflorum* *Clintonia uniflora*	*Podophyllum peltatum* *Impatiens biflora* *Eupatorium urticaefolium* *Arisaema triphyllum*

*Characteristic, though not present in the two hectares studied intensively

	Douglas fir-hemlock community	Oak community
C. MAJOR INFLUENTS	Euarctos americanus altifrontalis Felis concolor oregonensis Lynx rufus fasciatus Odocoileus c. columbianus Lepus americanus washingtonii Mustela cicognanii streatori Buteo borealis Otus asio brewsteri	Sylvilagus floridanus mearnsii Mustela frenata noveboracensis Buteo lineatus Otus asio naevius
D. MINOR INFLUENTS	Peromyscus maniculatus rubidus Microtus o. oregoni Clethrionomys c. californicus Scapanus o. orarius Sorex t. trowbridgii Penthestes rufescens Cyanocitta stelleri Hylocichla ustulata	Peromyscus leucopus noveboracensis Pitymys pinetorum scalopsoides Blarina brevicauda Cryptotis parva Penthestes atricapillus Cyanocitta cristata Hylocichla mustelina
E. SUBINFLUENTS (Invertebrates) (Gastropoda) (Centipedes) (Spiders) (Neuroptera) (Coleoptera)	Ariolimax columbianus Haplotrema vancouverense Oabius aiolus Hexura picea Theridion sexpunctatum Hemerobius pacificus Scaphinotus angusticollis Timarcha intricata Sciopithes obscurus	Philomycus carolinianus Haplotrema concavum Poaphilus kewinus Origanantes rostratus Micrathena gracilis Chrysopa plorabunda Amara impuncticollis Metriona bicolor Apion griseum

3. The soil of the oak community is richer in organic material as is shown by a comparison of soil-producing reactions of plants and animals.

4. The soil of the oak community is mixed more thoroughly by invertebrate animals since these are about twice as numerous in the deciduous as they are in the coniferous woods.

5. There are also nearly twice as many birds with soil-scratching and mixing reactions in the oak community.

6. In soil-making and mixing reactions, earthworms (Lumbricidae), Myriapoda, Collembola, mites, and moles in the Douglas fir-hemlock community have their equivalents in ants, Myriapoda, Collembola, mites, pine mice, and short-tailed shrews in the oak community.

7. Reactions modifying aerial factors are at least slightly more pronounced in the Douglas fir-hemlock community than in the oak community. In the summer the reduction of light intensity in the two communities appears to be similar, though data are incomplete. In the winter, however, the oak community is exposed to nearly full light intensity while the light in the Douglas fir-hemlock forest is decreased still more through the high proportion of cloudy days.
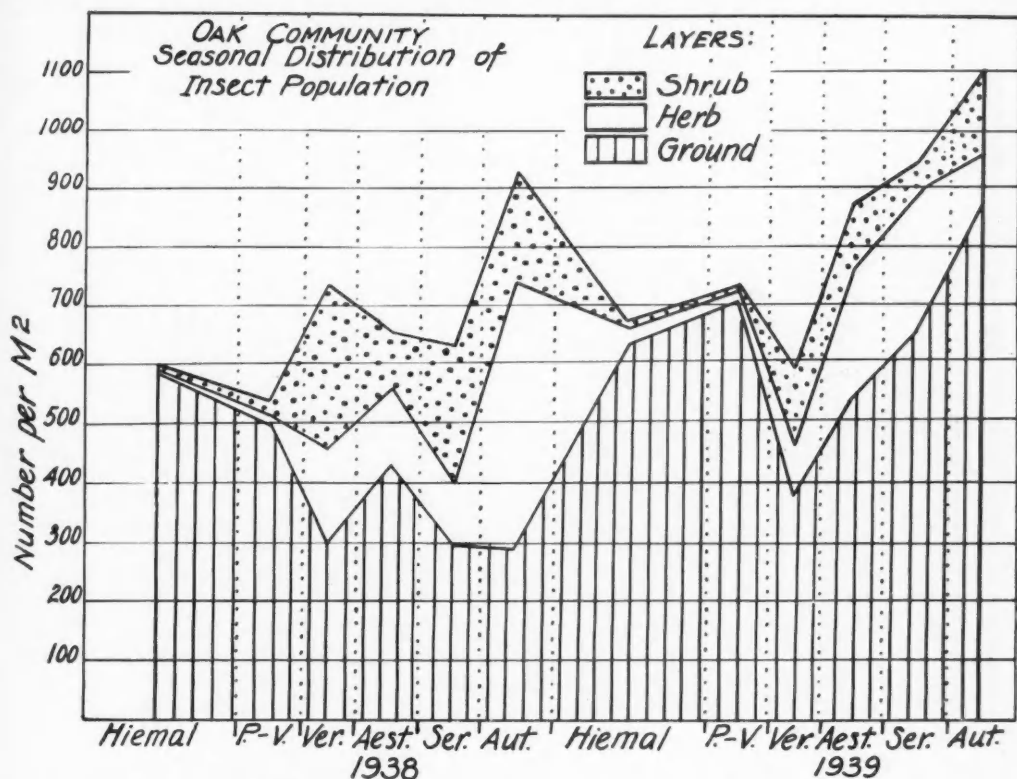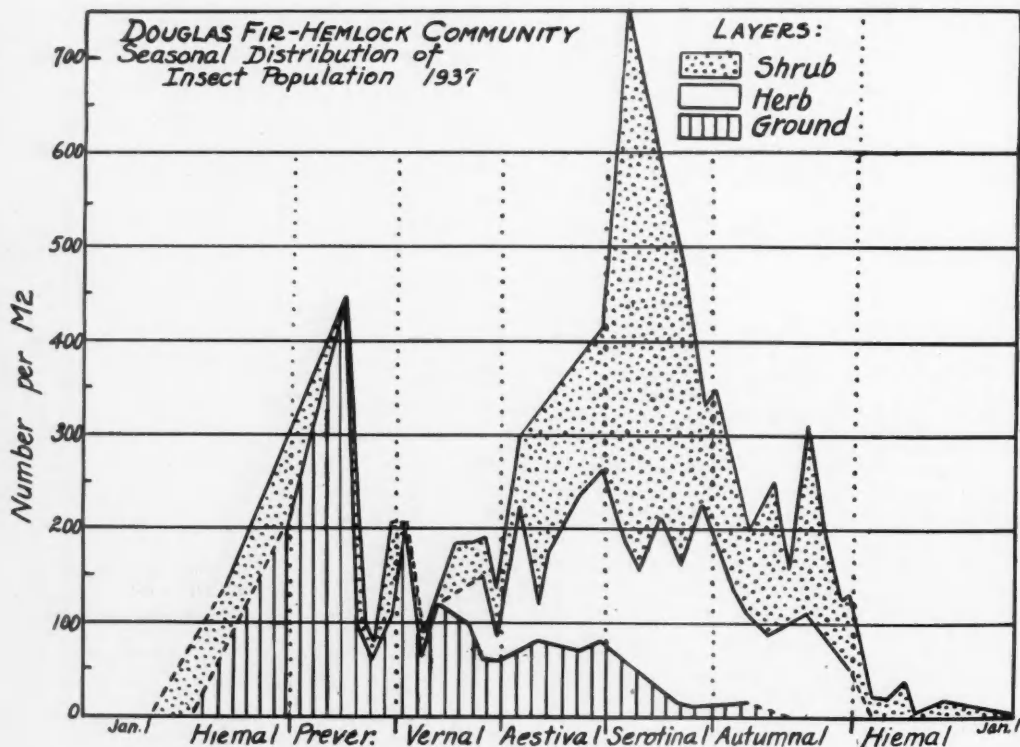

Fig. 10. Seasonal distribution of the insect population (exclusive of Apterygota) by strata for the Douglas fir-hemlock community for 1937. Population is expressed in terms of number of insects per square meter. Data obtained from Dr. James A. Macnab. See text.

8. Thermal blanketing by the vegetation is more pronounced in the coniferous forest especially during the winter seasons.

9. During the summer seasons, more bird species and individuals nest in the canopy and in cavities in the deciduous trees than in the coniferous. However, only about 50 percent of the birds in the oak community are permanent residents while approximately 85 percent of the Douglas fir-hemlock species are permanent residents.

10. Spiders are much more numerous in the Douglas fir-hemlock community than they are in the oak community.

11. In the Douglas fir-hemlock community aphids are the chief invertebrates which suck the juices from plants, while in the oak community aphids share this coaction with numerous leafhoppers, fulgorids, and Hemiptera.

12. In the coniferous forest there appears to be a close correlation between abundance of aphids and spiders; as the spiders increase in numbers during the summer the abundance of aphids decreases rapidly.

13. There are few species and individuals of leaf-eating beetles and Lepidoptera in the Douglas fir-hemlock community; these are numerous in the oak woods. Their abundance undoubtedly is correlated with the abundance of their food.

14. During the summer months the total insect population of the oak forest is approximately twice that of the Douglas fir-hemlock community. Correlated with this is the fact that insectivorous birds are much more numerous and varied in specific composition in the oak woods than they are in the Douglas fir-hemlock forest.

15. The proportional distribution of the total population of invertebrates (based on quantitative collections) is somewhat different in the two communities during the aestival and serotinal seasons.

	Douglas fir-hemlock community	Oak community
Arachnida....	31%	8%
Myriapoda...	8	1
Apterygota...	22	22
Homoptera...	10	7
Hemiptera.... less than	1	3
Coleoptera....	5	10
Diptera......	9	7
Hymenoptera.	4(few ants)	24(many ants)
Enchytraeidae	5	16
All others....	5+	2

16. In the summer seasons the oak community supports a more varied and abundant population than the Douglas fir-hemlock community.

	Douglas fir-hemlock community	Oak community
Birds, number effective daily per hectare........	20 (24 species)	35 (28 species)
Insects (other than Apterygota), individuals per M².	465	822
Total invertebrates, individuals per M².......	963	1573

17. Insects hibernate in the oak community in response to falling temperature and decrease in leaf shelter on the plants. This phenomenon, so far as observed, is largely lacking in the Douglas fir-hemlock community.

18. In the oak community the seasons are well defined by both plant and animal activities. Only the summer seasons have been studied for the Douglas fir-hemlock forest, but aspection appears to be somewhat different there.

19. The presence of northward migrating birds in the oak community is closely correlated with abundance of the kinds of food taken by the various species.

CONCLUSIONS

1. Mature coniferous and deciduous forest communities are very similar, for the plants and animals associated in them constitute ecologically equivalent groups which—together with the habitat factors—perform all essential dynamic processes.

2. The taxonomic composition of these ecologically equivalent groups differs greatly, in some cases, for the two communities.

3. The coniferous and deciduous forest communities are direct responses to the habitats affecting them; that is to say, the taxonomic variations of the two communities are the result of the physiological differences of the organisms comprising them.

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THE MARINE COMMUNITIES OF A TIDAL INLET
AT CAPE ANN, MASSACHUSETTS:
A STUDY IN BIO-ECOLOGY

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THE MARINE COMMUNITIES OF A TIDAL INLET
AT CAPE ANN, MASSACHUSETTS:
A STUDY IN BIO-ECOLOGY

INTRODUCTION

An ecological study of the marine communities inhabiting a tidal inlet was made over a period of five years to determine the nature of their organization and dynamics. Field studies were conducted during the summer months of the years 1933 through 1937 over an annual period of eleven weeks. Brief visits were made in December of 1933 and March of 1934 for an examination of winter conditions, and additional observations were made during the month of August in 1938 and 1940. The problem was confined for the most part to the communities of an inlet known as the Annisquam River, located at Cape Ann, Massachusetts. The viewpoint of bio-ecology, or synecology, prevailed throughout the study. All common plants and animals were considered together as interlocking components of one natural unit. Life history studies were confined to those phases concerned directly with interrelationships.

Community composition was studied in reference to the physiographic features of the habitats and to the tidal flow and ebb. The ecological processes which received especial attention were those of interrelationships between organisms (coactions), of rhythmical changes produced by tidal fluctuations, of seasonal and annual changes, and of physiographic succession.

Many studies have been published on the marine life of the littoral region. The earlier works were taxonomic or faunistic in nature. Faunistic surveys soon gave way to problems of zonation and distribution and their correlation with physical factors of the environment. It is only within recent years that marine communities have been analyzed as biotic units having sociological properties as well as physical relationships to the environment (Gislen 1930).

The writer is deeply indebted to Prof. Victor E. Shelford, under whose direction the problem was carried out, for guidance in conducting the field studies and in preparing the manuscript. He is also indebted to Prof. C. E. Gordon and Prof. H. E. Warfel for suggestions and aid in the early part of the survey; to the family of the Rev. Dr. J. W. Beardslee for field assistance, especially to the Rev. W. A. Beardslee for aid in conducting the dredging operations and for information on birds; to Mr. F. S. Speck for field assistance; to Mr. Carl Freiburg for information on fishes; to Dr. C. L. Kanatzar for plankton examinations; to Capt. John Alvord for use of his diving helmet; to Mr. G. H. Colman for loan of scientific apparatus; to the Rev. R. M. Barker for meteorological data; to the Gloucester Station, United States Fish and Wildlife Service, for hydrographic data; to the United States Army District Engineer Office at Boston for topographic maps and information; to the Massachusetts State Bureau of Marine Fisheries for information on work of the bureau at Cape Ann; to Mr. N. W. Montgomery for boat and field-base accommodations; to the members of the departments of zoology and botany, Massachusetts State College, who assisted with the identification of organisms; and to the following who corrected the nomenclature for the revised manuscript: Dr. W. L. Schmitt, annelids and crustaceans; Dr. W. J. Clench, mollusks; Dr. C. L. Hubbs, fishes.

REGION OF STUDY

GEOGRAPHY AND GEOLOGY

Cape Ann is a promontory which lies at the northern extremity of Massachusetts Bay. It is approximately 23 miles northeast of Boston Harbor. The narrow inlet known as the Annisquam River cuts off
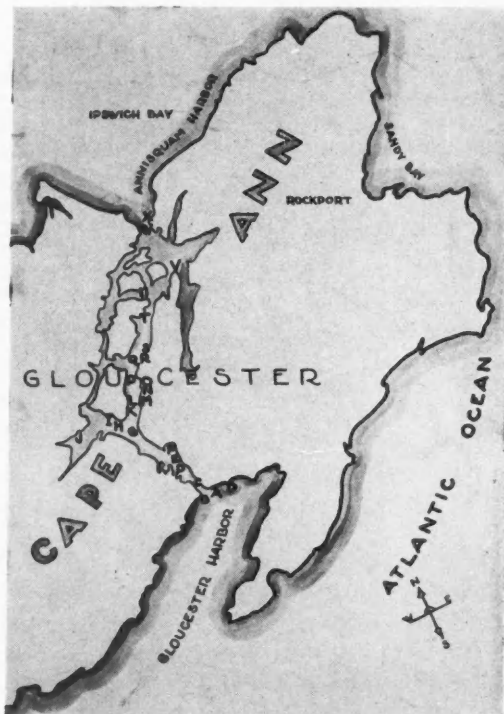

Fig. 1. Map of Cape Ann, Massachusetts. Letters indicate location of field stations.
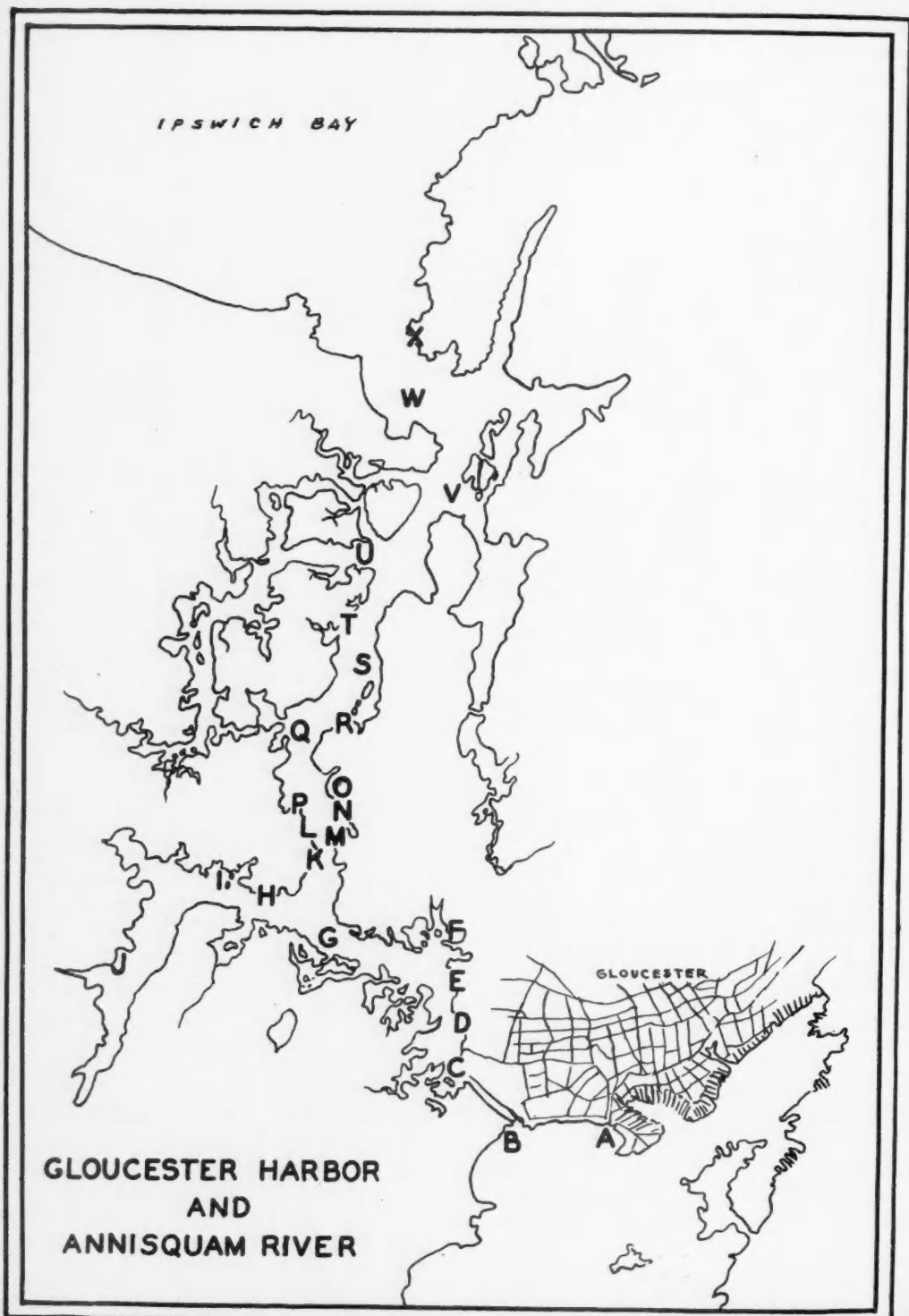
FIG. 2. Topographic map of the Annisquam Inlet. Letters indicate location of field stations. From U. S. C. and G. S. map 233.

the eastern end of the promontory, making it an island. This inlet, or strait, is 3.5 nautical miles in length (approximately 4 land miles) measured along the channel way, and has an average width of 175 yards. It connects the waters of Gloucester Harbor on the south with those of Ipswich Bay on the north. The island, on which is located the city of Gloucester and the town of Rockport, lies between longitudes 70°35′ and 70°41′ and between latitudes 42°35′ and 42°42′. (Figs. 1, 2; United States Coast and Geodetic Survey maps 233 and 243.)

Cape Ann is a massive ledge of granite and syenite rock, the surface of which has been glaciated and is now a terminal moraine covered with glacial drift. According to Shaler (1889), Cape Ann was an island at the close of the last glacial period, the dividing strait having been produced by the action of the glacier on weaker rocks. Later, deposition of sediments at the southern end of the inlet closed it at this point; subsequently, marshes developed behind this bar in the closed inlet to the northern entrance, which alone remained open. Upon the advent of colonization by the white man, an artificial canal was constructed in 1643 across the neck of land which had been deposited. This canal was blocked by deposits from violent storms in 1704 and again in 1723. Nearly a century later the inlet was reopened by the construction of a canal 600 yards long. Accumulating sediments gradually closed it once more until the state government took over the jurisdiction of the waterway in 1903 and reopened it for navigation. Thus, the island condition of the eastern end of Cape Ann was restored. More recently, a bar has been formed across the northern entrance at Annisquam, but it has not yet blocked the inlet, although it has become necessary to dig a channel through one end to allow the passage of large boats during low water.

There has been dispute in the geological literature of this region as to whether the promontory is rising or sinking. Much evidence has been presented on both sides of the question. The writer is inclined to believe that sometime after the last glacial period Cape Ann was elevated some 40 to 60 feet above the former shore level (Tarr 1903); but since that time it has come to have a sinking coastline (Shaler 1889; Penhallow 1907). Penhallow (ibid.) reported that

the Atlantic coast was sinking at the rate of two feet every one hundred years, but more recently McAtee (1935) has stated that the subsidence is about one foot in a hundred years. In any event, deposition has been and is now taking place in the inlet at such a rate that it would eventually fill the inlet completely if left undisturbed. Sand and silt deposits have formed bars, beaches, flats, and marshlands. Rocky shores have been produced by glacial deposits and by weathering of adjacent ledges.

There are several small streams of fresh water that enter the strait, but nowhere does fresh water enter the waterway of Annisquam River in sufficient quantity to produce significant brackish conditions and the marine communities maintain their dominance to the limits of the high-tide level. The present study is the first of its kind to be conducted in this region.

METEOROLOGY

The general climatic conditions of Cape Ann are given in Table 1 which summarizes the temperature and rainfall records during the five years of this study. These measurements were recorded by the Rev. R. M. Barker, who operates a cooperative Weather Bureau Station at Gloucester.

Cape Ann has a temperate climate, but the winter season at times is quite rigorous. The intervening winter periods during the term of this research might be characterized as follows: 1933-34, very severe (the inlet was frozen from end to end); 1934-35, severe; 1935-36, severe; 1936-37, mild.

HYDROCLIMATE

During the summers of 1935-37, physical measurements were made on the waters of the inlet to determine in part the hydrographic environment of the marine communities. Water temperature, density, salinity, hydrogen ion concentration, and oxygen content were measured in the surface waters, for the most part those that covered the tidal zone. Additional information has been obtained from the Gloucester Station of the United States Fish and Wildlife Service located on Ten Pound Island at which has been made a record of the temperature and density of the water in Gloucester Harbor. Table 2 summarizes the hydroclimatic conditions of the inlet.

TABLE 1. Summary of Climatic Conditions, 1933-1937.

	1933		1934		1935		1936		1937	
	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.
Mean Temperature, °F......	47.3	....	45.9	....	46.7	....	47.6	....	49.1	....
Annual Rainfall, In.........	....	58.8	....	43.8	....	46.0	....	54.1	....	49.1
June-August Mean, °F......	65.5	....	65.1	....	66.6	....	66.6	....	68.4	....
June-August Mean, In.......	....	2.57	....	2.15	....	4.09	....	3.95	....	3.54
Monthly Maximum.........	66.3 Aug.	10.26 Apr.	68.3 July	7.89 Sept.	69.5 July	8.76 June	67.6 July	9.01 Dec.	72.0 Aug.	7.25 Apr.
Monthly Minimum.........	26.1 Dec.	1.28 Nov.	16.2 Feb.	1.07 Aug.	22.1 Jan.	0.31 Oct.	22.0 Feb.	1.53 May	28.9 Dec.	0.99 July

TABLE 2. Summary of Hydrographic Conditions, Summers of 1935-1937.

	Air Temp.	Water Temp.	pH	Density	Salinity 0/00	Oxygen cc/liter
1935						
Maximum......	30.5°C.	24.0°C.	8.2	1.025	34.61	7.20
Minimum......	16.0	14.5	7.6	1.021	29.69	3.54
Average.......	23.2	19.5	7.8	1.022	31.70	4.90
1936						
Maximum......	33.0	23.5	8.3	1.023	32.94	7.94
Minimum......	17.0	16.0	7.6	1.020	28.77	3.74
Average.......	22.5	20.4	7.8	1.022	31.03	4.96
1937						
Maximum......	29.5	24.0	8.2	1.024	34.13	5.79
Minimum......	17.0	17.0	7.7	1.020	28.47	3.69
Average.......	23.6	20.8	7.9	1.022	31.83	4.89

Water temperatures were taken at the surface. The daily water temperature fluctuates within a narrow range throughout the summer days, and the means of the three season's records agree fairly well, averaging 20° C. The water of the inlet is usually between two and three degrees warmer than the water of Gloucester Harbor. This relationship is noted by comparing daily readings as well as the monthly and seasonal averages. The shallowness of the inlet and the warming effect of the exposed tidal zone undoubtedly explain this difference in temperature. The density of the water was measured by means of a hydrometer. The samples of water were taken from the surface at those locations where temperature readings were made. The density and corresponding temperature measurements were used to compute the total salinity by an application of Knudsen's hydrographic tables. The average density each season was 1.022 while the average salinity was 31.18 °/₀₀. The hydrogen ion concentration was determined with a colorimetric set employing phenol red as the indicator and a quinhydrone electrometric set. The readings show a range of 0.6 and a mean of pH 7.8. The amount of dissolved oxygen in the water was determined by the Winkler method. The samples were taken from a level approximately one foot below the surface of intertidal waters. The range in oxygen content throughout a season was considerable, but the averages of each year's samples compare very closely. The mean oxygen content of all samples analyzed was 4.92 cc. per liter.

After the restoration of the original inlet by the construction of a canal, a peculiar tidal current was produced. During the incoming tide, ocean water now enters both ends of the inlet, from Gloucester Harbor and Ipswich Bay. These currents flow toward each other converging at the channel known as Little River, into which both currents of water flow. During the outgoing tide the water of Little River runs out into both channels, and diverges at the junction into two currents that flow in opposite directions, to be emptied into Gloucester Harbor and Ipswich Bay. The velocity of the current depends on the height of tide, the direction and velocity of the wind, and the width of the inlet at various points. At times of spring tides, and with strong winds of the late summer, the waters flow quite rapidly, often with large

waves and white caps. At narrow passages, especially at the canal and beneath the railroad bridge, the current is very great at times. Ordinarily the surface is quite calm, and the velocity ranges up to two miles per hour. The greater bulk of the water in the strait is changed with each tide, keeping hydroclimatic conditions fairly uniform throughout. The mean rise and fall of the tidal level at Annisquam is 8.5 feet, while at Gloucester Harbor it is 8.7 feet. The range in spring tides is 9.9 and 10.1 feet, respectively. The high water interval is 11 hours and 14 minutes. (Information from United States Engineer Office at Boston.)

FIELD STATIONS

INTERTIDAL STATIONS

Twenty-four stations were established along the inlet from the shores of Gloucester Harbor on the south to those of Annisquam Harbor on the north. These sites were selected to include all of the major types of communities and habitats, and spaced as uniformly as conditions would permit. Eleven stations were placed on either side of the inlet and two on bars in the middle of the channel. Fifteen were studied quantitatively by use of quadrats placed at certain levels, while nine were used for general and comparative observations. For the most part, a station extended from high-water to low-water line, even though several communities were often included in this range. In other cases a restricted area was set to include only one community. Reference should be made to the maps of the inlet (Figs. 1, 2) to obtain the exact location of each station. Shallow tidal pools were found only among the rocks at the extremities of the inlet (Stations B and X) and occasionally on the high marshes where holes had been dug. Consequently they did not play an important part in the community relations of these shores. Breakers and surf were also restricted to the harbor and bay shorelines (Stations A, B, X) and with these exceptions were not important factors. Table 3 gives a summary of the intertidal stations.

SUBTIDAL STATIONS

Three distinct channels were recognized in the study of subtidal bottom communities. The southern channel extends from Gloucester Harbor to Little River (Fig. 3); the northern channel extends from Ipswich Bay to Little River; and Little River itself is the third, formed at the union of the other two. Environmental conditions in the strait are quite uniform except for the character of the bottom and the varying velocities responsible for these differences. The bottom materials along Little River and the southern channel are fine mud (clay) deposits, for the most part, with occasional mixtures with sand along the lower, main channel, and a section of shelly, rocky bottom to the north of the railroad bridge at Station E, where the current is stronger as it passes through a narrow channel. Along the northern inlet the bottom is composed chiefly of local stretches of mud (particularly in the broader sections), of sand,

TABLE 3. Intertidal Field Stations.

Station	Substratum	No. of quadrat levels with horizontal distances in feet and vertical distances in inches between quadrats.
A	Sea-wall at about M.H.W.L.; Coarse sand on higher level; gravel and pebbles on lower beach	
B	Sea-wall near M.H.W.L.; Gravel bank below wall; small rocks and boulders extending to large boulders at M.L.W.L.	(1) Gravel bank; (2) 30 ft., 42 in.; (3) 20 ft., 4 in.; (4) 50 ft., 6.5 in.; (5) 21 ft., 0 in.; (6) 21 ft., 3.5 in.; (7) 21 ft., 6.5 in.; (8) 15 ft., 7 in.; (9) 15 ft., 4 in.; (10) 15 ft., 6 in. - near S.L.W.L.
C	Steep bank of rock fragments and boulders.	
D	Mud flat with black silt depression on landward side and firm, sandy-mud on channel side.	
E	Mussel bed on a bar beneath a railroad tressel.	(1) Base of sea-wall; (2) 16 ft., 28.5 in.; (3) 36 ft., 13.5 in.; (4) 36 ft., 17.5 in.; (5) 4 ft., 5 in.; (6) 2 ft., 10 in.; (7) 2 ft., 10 in. - near S.L.W.L.
F	Marsh bank and muddy creek adjoining main channel.	
G	Bar in middle of inlet; One end sandy, other muddy.	(1) Near top of bar; (2) 40 ft., 7 in.; (3) 30 ft., 5 in.; (4) 22 ft., 7 in.; (5) 22 ft., 5 in.; (6) 22 ft., 10.5 in. - near S.L.W.L.
H	Ledge of solid rock.	
I	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 16 ft., 31.5 in.; (3) 16 ft., 37.5 in.; (4) 21 ft., 14 in.; (5) 21 ft., 14 in.; (6) 21 ft., 10 in.; (7) 16 ft., 8 in.; (8) 16 ft., 5 in.; (9) 16 ft., 4 in.; (10) 16 ft., 5 in.
J	High marsh, low marsh, and mud flat.	(1) Near S.H.W.L.; (2) 21 ft., 4 in.; (3) 21 ft., 1.5 in.; (4) 26 ft., 1.5 in.; (5) 40 ft., 4.5 in.; (6) 14 ft., 52 in.; (7) 21 ft., 25 in.; (8) 21 ft., 7 in.; (9) 21 ft., 1 in.; (10) 20 ft., 2 in.; (11) 20 ft., 3 in.
K	Ledge with weathered boulders and rocks.	(1) Near M.H.W.L.; (2) 6 ft., 14.5 in.; (3) 4 ft., 15 in.; (4) 7 ft., 17.5 in.
L	High marsh and low marsh.	(1) Near M.H.W.L.; (2) 25 ft., 18.5 in.; (3) 25 ft., 31 in.
M	Ledge and steep talus slope.	(1) S.H.W.L.; (2) 6 ft., 57.5 in.; (3) 5 ft., 19.5 in.; (4) 5 ft., 17.5 in.; (5) 5 ft., 12.5 in.
N	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 25 ft., 30.5 in.; (3) 6 ft., 27 in.; (4) 26 ft., 11 in.; (5) 31 ft., 3.5 in.; (6) 21 ft., 1 in.; (7) 16 ft., 2 in.
O	Tidal creek with steep marsh banks and soft muddy bottom.	
P	Ledge and steep talus slope of large boulders.	(1) S.H.W.L.; (2) 6 ft., 22 in.; (3) 6 ft., 28 in.; (4) 6 ft., 36 in.; (5) 6 ft., 36 in.
Q	High marsh, low marsh, and mud flat.	(1) Near M.H.W.L.; (2) 12 ft., 35.5 in.; (3) 12 ft., 22 in.; (4) 40 ft., 8.5 in.; (5) 26 ft., 5.5 in.; (6) 16 ft., 3 in.; (7) 16 ft., 6.5 in.
R	Ledge with boulders.	(1) Near M.H.W.L.; (2) 5 ft., 24.5 in.; (3) 6 ft., 25.5 in.; (4) 4 ft., 8 in.
S	Sand bar in middle of inlet. One side is developing into a muddy lagoon.	(1) Top of bar; (2) 16 ft., 7 in.; (3) 16 ft., 4 in.; (4) 21 ft., 3 in.; (5) 21 ft., 3.5 in.; (6) 21 ft., 2 in.; (7) 21 ft., 2.5 in.; (8) 21 ft., 1 in.
T	High marsh and pile of large boulders.	(1) Just above M.H.W.L.; (2) 10 ft., 6.5 in.; (3) 16 ft., 24 in.; (4) 6 ft., 9 in.; (5) 4 ft., 9 in.; (6) 4 ft., 16.5 in.; (7) 4 ft., 13.5 in.; (8) 4 ft., 15.5 in.
U	High marsh plateau.	
V	Mussel bed over a mud flat.	
W	Extensive sandy beach.	(1) Near M.H.W.L.; (2) 20 ft., 8 in.; (3) 40 ft., 8 in.; (4) 20 ft., 6 in.; (5-18) 26 ft. apart with vertical distances of: 5.5, 4, 3.5, 2.5, 3, 1, 12.5, 6.5, 4, 6, 6, 4.5, 12.5 in.
X	Ledge and pile of large boulders. Sand deposits and tidal pools among rocks.	

FIG. 3. Section of the inlet at mean-high-tide looking northwest from near station E.

and of mixtures of sand and mud with an occasional outcropping of rocks.

The subtidal bottom is smooth and firm except in a few regions of fine mud deposits. The central channel is narrow, winding and steepsided. Much of it has been dredged to a uniform depth of eight feet at mean-low-water, and for a width varying between 50 and 200 feet. The maximum depth is not over 34 feet at mean-low-water. (See maps of the United States Engineer Office, Boston, Mass. "Gloucester Harbor and Annisquam River." File 140, 141 Dr. 37 and "Annisquam River, Mass." File 168, 168 Dr. 37.)

METHODS AND TERMINOLOGY

For the most part, the field work was conducted on a quantitative basis. The intertidal communities were investigated by means of quadrat sampling. A counting frame twenty inches square was applied at selected levels at the various established stations for a sampling of the plants and animals existing at those levels. The depth of each quadrat sample varied with the substratum. In general, rocky shores were studied to the bottom of the removable rocks, while sandy and muddy habitats were dug to a depth of about ten inches. During two seasons of the field work, a quadrat ten inches square was used when it was learned that the smaller one gave as representative a sample of the common organisms and was more expedient for field use. All of the data have been adjusted to read in terms of abundance on 400 square inches or approximately one-quarter of a square meter. The square meter quadrat used by some workers was found to be altogether too large for this intertidal study because of the great density of organisms found, and the fact that it would cover too much vertical distance (Dexter 1943). A total of 432 quadrat counts was made. These were supplemented by general observations and general samplings made over the entire area.

The subtidal bottom communities were studied with the aid of a naturalist's dredge, constructed of an

iron frame resting on runners and carrying a large bag of medium netting with an end base of canvas. The dredge was dragged along the bottom of the inlet from a small boat propelled by an outboard motor. Each haul was recorded separately and quantitatively. These bottom samples were supplemented by observations on the bottom communities from a diving helmet (Dexter 1942).

Plankton samples were taken with a fine bolting-cloth net. Fishes were observed from docks and collected with the dredge net and with a dip net. Additional information was secured from local fishermen. Birds were observed in the field, and information was also obtained from a number of persons who had kept records of the birds in this region.

Coactions were determined by direct observations in the field and experimentally by the use of aquaria. Movements were studied, especially of snails, by observing the progress of marked specimens.

The ecological nomenclature follows the concepts and definitions established by Shelford (1931, 1932). Because of the lack of uniformity in the use of ecological terms, and the confusion which has arisen from the use of various systems, and, in some cases, the failure to recognize ecological concepts, it becomes necessary to give briefly the terms and their definitions as used in this paper.

Biome—the largest community recognized as a unit. Consists of two or more related associations and their developmental stages.

Association—a climax community of relatively uniform taxonomic composition and physiognomy.

Faciation—a portion of an association based upon a grouping or an absence of some of the predominant species.

Sere—the sequence of successional stages from the initial to the climax condition.

Associes—a developmental community which is undergoing gradual change. Any level in a sere below the climax.

Predominants—plants and animals which are abundant and significant in the community.

Dominants—species which control and characterize the community directly or through their effects on the habitat. They are the common, large, sedentary, or slow-moving forms.

Subdominants—species having minor control of the community. They are neither as abundant nor as uniformly distributed as the dominants, but locally may take the place of dominants.

Influents—species which are significant in the community because of their importance in the food chain.

Subinfluents—less important than influents in the dynamics of the community because of less abundance, smaller size, or lack of importance in the food chain.

Permeant Influents—wide ranging, motile animals which produce significant changes, chiefly through predation.

Secondary Forms—plants and animals of minor importance.

Incidentals—species of no significance in the economy of the community.

COMMUNITIES

The earlier works on marine life of the Atlantic coast were developed from the point of view of faunal zoogeography (Sumner 1908; Murray & Hjort 1912; Sumner, Osburn, & Cole 1913). The latter publication demonstrates that Cape Cod is a faunal barrier, 55% of the fauna of the Woods Hole region being south ranging and 30% north ranging. On this basis the Woods Hole region is designated as part of the "Virginian" province while north of Cape Cod the fauna is characteristic of the "Arcadian Province." Murray & Hjort (1912) described the coast from Cape Cod to Northern Newfoundland as "Boreo-arctic." Analysis of the common macroscopic marine life at Cape Ann, so far as distribution is known, shows that 11.8% is north ranging or "Arcadian," 6.7% is south ranging or "Virginian," and 81.5% is found for considerable distances both north and south of Cape Cod. This indicates that the littoral biota of Cape Ann is within the "Arcadian" province although obviously the dividing line cannot be as sharp as formerly believed. In general, however, one can agree with Sumner et al. (1913) that "Cape Cod does have appreciable influence as a barrier."

The more recent studies have been concerned with the aggregations of marine life, and investigators are realizing more and more the necessity of a dynamic point of view on community relationships (Shelford & Towler 1925; Bigelow 1930; Shelford 1931, 1932; Allee 1934; Vaughan 1934; Taylor 1935; Rees 1939; Clements & Shelford 1939). Shelford declared succinctly (1930a) that "modern ecology may be stated to be the science of communities" and Allee (1934) has pointed out that "the distinctive contribution of ecology to biological complex has been the emphasis on the fact that organisms live in communities."

In pursuing this approach in the study of marine communities, however, an interesting difference of opinion has developed in regard to the relative importance of certain factors. Some workers have over-stressed the importance of the physical environment, in some cases assigning community control to a single factor. Others have lost sight of the community in the details of life histories of the individual species. The most desirable approach seems to be a balanced point of view including consideration of environmental influences, physiological life histories, and coactions of organisms in proper perspective. As Shelford (1931) has pointed out, sometimes biotic factors control, and at other times, physical factors control. It might be added that only by a complete analysis of each situation can we come to understand the natural laws governing biotic communities.

As the best yet devised and most convenient method of designation, the system long in use of naming

communities after several of the dominant or characteristic species (Peterson 1918) has been adopted here. The naming of certain ones of the following communities follows that of Newcombe (1935) as far as feasible, but because of differences in the composition of the communities between Cape Ann and the Bay of Fundy, where Newcombe did his work, it has become necessary to modify his system somewhat. Also, we are here concerned with the communities of a protected inlet which are somewhat different from those of the exposed ocean shores. It should be borne in mind that all of these designations of marine communities are provisional and subject to change with additional research on the study of community organization. The annual fluctuation of the status of some species necessitates a change in their ecological evaluation so that the naming of a fluctuating dynamic system, such as a marine coastal community, has significance only in relation to time and place. Not until an extensive ecological survey is made of the entire northeastern coast of the Atlantic Seaboard such as Shelford (1935) organized for the Pacific coast will it be possible to assign definite names and rank to the marine communities with certainty.

The writer does not agree with MacGinitie (1939) that communities should be named after the particular place where one happens to study them, or that they should be named, as by common practice, after the zones of algae. It is now known that the animal populations are not always distributed according to zones of seaweeds and a geographic name as suggested by MacGinitie would not convey any meaning in regard to the nature of the community. When one realizes that the use of generic names of the controlling and characteristic species to designate a community refers only to the organization of that community at the time of study, MacGinitie's objection on the basis of significant seasonal and annual changes is dispelled. With such changes, a new community naturally comes into existence and demands a new name as well as a new analysis. By retaining a geographic name, there would be added confusion.

The plankton-nekton of the Annisquam inlet is a portion of one biome, while over the bottom and the tidal zone of this area, according to one point of view, there exist portions of three other marine biomes. In addition, there are two major communities transitional to land conditions.

PELAGIC COMMUNITY

CLUPEA-SYNGNATHUS FACIATION

The pelagic community of the Annisquam inlet is essentially the same as that described for the shallow water of Ipswich Bay (Dexter 1944), which is a portion of the Scomber-Calanus Biome. The Clupea-Syngnathus Faciation of the inlet, however, lacks the larger animals such as the tuna *(Thunnus thunnus)*, mackerel shark *(Isurus punctatus)*, and the finback whale *(Balaenoptera physalus)*. The following organisms are known to be among the most important of the larger pelagic species of the inlet: mackerel *(Scomber scombrus)*; herring *(Clupea harengus)*;

pipefish *(Syngnathus peckianus)*; pollack *(Pollachius virens)*; alewife *(Pomolobus pseudoharengus)*; butterfish *(Poronotus triacanthus)*; bluefish *(Pomatomus saltatrix)*; silver hake *(Merluccius bilinearis)*; smelt *(Osmerus mordax)*; common squid *(Loligo pealii)*; harbor seal *(Phoca vitulina)*; and jellyfishes *(Aurelia aurita, Cyanea capillata)*. The common tern *(Sterna hirundo)* and the belted kingfisher *(Megaceryle alcyon)* also became members of this community when they dive into the water for food.

The plankton was examined but not studied in detail. Diatoms, protozoans, microcrustaceans, and crustacean larvae constituted the more common organisms taken in the samples, but the bulk of the suspended material collected was detritus. The large amount of detritus and low concentration of plankton organisms in the water are accounted for by the facts that collecting was done for the most part in the shallow submerged tidal zone, and during the annual plankton minimum (July-August). A plankton sample taken on September 16, 1945, for a period of 15 minutes from a strong, outgoing current gave the following results: *Calanus finmarchicus*, abundant; fragments of green algae, common; ostracods, common; nauplius larvae, common; mysid larvae, numerous; veliger larvae, numerous; rhabdocoel turbellarian, numerous; clam seed, numerous; fragments of bryozoan and hydrozoan colonies, several; hydrozoan jellyfish, 2; detritus, abundant. The copepod *Calanus finmarchicus* is probably the most important of the plankton organisms. Large jellyfishes usually appear late in the summer in great quantities and constitute a conspicuous part of the plankton during a brief period. Within Aurelia and Cyanea there are found at times crustacean commensals of the genus Hyperia. *Aurelia aurita* was not recorded in 1933, but was carried into the inlet in great abundance in 1934, and was collected in decreasing numbers each succeeding year. *Cyanea capillata* was not seen during this study until 1935, when numerous specimens were swept in by the current. This was repeated in 1936, but in small numbers only in 1937.

SUBTIDAL BOTTOM COMMUNITY

LAMINARIA-CANCER FACIATION

General Character

The subtidal bottom community of the inlet is similar to the bottom community of Ipswich Bay (Dexter 1944). The shallow inlet is a part of the Strongylocentrotus-Buccinum Biome, but it lacks most of the large gastropods *(Buccinum undatum, Neptunea decemcostata, Colus stimpsoni)*, two of the kelps *(Agarum cribrosum, and Laminaria longicruris)*, the larger bottom fishes *(Melanogrammus aeglifinus, Hippoglossus hippoglossus)*, and one of the red algae *(Corallina officinalis)*. Also, some of the predominants of the bay region are less important or seldom found in the inlet.

Some of the bottom invertebrates found in the bay but not dredged in the Annisquam River are the bivalves *Arctica islandica, Modiolus modiolus;* the decapods *Libinia emarginata, Palaemonetes vulgaris;*

and the starfish *Henricia sanguinolenta*. The fol-
lowing predominants of the bay are present but less
important in the inlet: *Echinarchnius parma, Euthora
cristata, Chondrus crispus,* and *Lacuna vincta.* On
the other hand, some species are more abundant and
ecologically significant in the inlet than in the bay.
Among these are the algae *Laminaria digitata, Chae-
tomorpha linum;* the mollusks *Polinices heros, Nas-
sarius trivittata, Littorina littorea, Mytilus edulis;*
the crustaceans *Cancer irroratus, Carcinides maenas,
Pagurus longicarpus, Crago septemspinosus;* the
arachnoidean *Limulus polyphemus;* and the fishes
Fundulus heteroclitus, Anguilla bostoniensis. The
inlet community is designated as the Laminaria-Can-
cer Faciation, being characterized by *Laminaria
digitata, L. Saccharina* (brown algae), and *Cancer
irroratus* (rock crab). Previous to 1933, there existed
a Zostera (eel-grass) Faciation, which was destroyed
with the virtual disappearance of this plant from the
Atlantic coast in 1932. (See Dexter 1944a, 1945, and
1946 for discussion of this problem at Cape Ann.)
A total of 110 dredge hauls was made in the three
channels over a period of four seasons.

The evaluation of the members of this community
follows the criteria as established for the study of
Ipswich Bay (Dexter 1944, p. 354). The first num-
ber following each species is the maximum taken in a
single dredge haul, which in most cases covered an
area of about 1,610 square feet (approximately 60
square meters). The second number is the percent-
age of occurrence in the dredge hauls. Thus, *Asterias
vulgaris,* 41/98 signifies that up to 41 specimens of
this species were collected at one time, and that the
species was collected in 98% of all the dredge hauls.

Dominants and Slow-Moving Influents
Dominants
Asterias vulgaris, starfish, 41/98
Polinices heros, sand-collar snail, 12/40
Strongylocentrotus drobachiensis, green sea urchin, 2/10
Ulva lactuca, sea lettuce, 13/74
Laminaria digitata, kelp, 7/38
Laminaria saccharina, kelp, 4/32
Urophycis chuss, squirrel hake, 7/30
Pseudopleuronectes americanus, winter flounder, 5/18
Myoxocephalus scorpius, shorthorn sculpin, 2/14
M. octodecemspinosus, longhorn sculpin, 1/4
M. aeneus, little sculpin
Subdominants
Chaetomorpha linum, green alga, Abun./52
Raja erinacea, little skate
R. diaphanes, big skate
Urophycis tenuis, mud hake
Lophopsetta maculata, sand flounder
Influents
Mytilus edulis, blue mussel, 25/40
Nassarius trivittata, sand snail, 80/26
Littorina littorea, periwinkle, 30/38
Gammarus locusta, amphipod, 18/44
Caprella acutifrons, amphipod, 15/30
Lepidonotus squamatus, scale worm, 4/38
L. sublevis, scale worm, 5/10
Chondrus crispus, Irish moss, 2/26
Euthora cristata, red alga, Many/20
Lumbrinereis tenuis, annelid, 4/20

Subinfluents
Lacuna vincta, snail, 15/12
Gemma gemma, bivalve, 9/20
Chalina oculata, finger sponge, 9/26
Isopods (unidentified), 10/36
Amphipods (unidentified), 8/16
Neopanope sp., mud crab, 4/12
Syngnathus peckianus, pipefish, 1/8
Crepidula fornicata, boat shell, 34/6
Sertularia pumila, hydroid, 20/26
Abietinaria abietina, hydroid, 16/38
Bugula turrita, bryozoan, 5/44
Permeant Influents
Cancer irroratus, rock crab, 51/64
Pagurus longicarpus, hermit crab, 39/30
Carcinides maenas, green crab, 37/14
Crago septemspinosus, shrimp, 40/48
P. pollicaris, hermit crab, 17/8
Limulus polyphemus, horseshoe crab, 3/20
Anguilla bostoniensis, eel, 1/2
Tautogolabrus adspersus, cunner, 1/4
Poronotus triacanthis, butterfish, 1/2
Fundulus heteroclitus, minnow
Osmerus mordax, smelt
Pholis gunnellus, rock eel
Homarus americanus, lobster
Secondary Forms
Metridium dianthus, sea anemone, 14/10
Obelia spp., hydroids, 12/20
Ophiopholis aculeata, brittle star, 4/6
Lichenophora hispida, bryozoan, 12/26
Molgula manhattensis, sea squirt, 16/10
Spirorbis spirorbis, serpulid worm, 12/6
Bryozoan (unidentified, encrusting forms), 10/30
Tubularia spectabilis, hydroid, 8/12
Crepidula plana, snail (commensal with Pagurus), 10/10
Saxicava arctica, bivalve, 3/10
Echinarchnius parma, sand dollar, 3/4
Tellina tenuis, bivalve, 5/6
Hydractinia echinata, hydroid (commensal with Pagu-
rus), 3 sq. in./16
Botryllus schlosseri, sea quirt, 5 col./12
Balanus eburneus, barnacle, 3/6
Nereis pelagica, clam worm, 2/6
Rhodymenia palmata, red alga, 2/8
Siliqua costata, sand bar clam, 1/8
Idothea baltica, isopod, 1/6
Cerastoderma pinnulatum, bivalve, 1/6
Aeginia longicornis, isopod, 1/5
Chorda filum, sea chord, 1/5

Community Organization and Coactions

Dredging operations conducted along the entire
channel-way and observations on the bottom from a
diving helmet and from the surface over shallow
areas as spring-low-tides have shown this Laminaria-
Cancer Faciation to be as follows.

On the sandy and sandy-mud bare sediments of the
channel floor are found many transient animals:
Cancer, Pagurus, Carcinides (crabs); Polinices
(snail); Limulus (horseshoe crab); Cargo (shrimp);
and a number of ground fishes, chiefly the squirrel
hake (Urophysis); flounder (Pseudopleuronectes);
sculpins (Myoxocephalus); skates (Raja); and the
eel (Anguilla). Also, the less rapidly moving animals,
Asterias (starfish), Strongylocentrotus (sea urchin),
and Echinarchnius (sand dollar) wander over the

surface. In the substratum are amphipods, annelids, and bivalves (Tellina, Cerastoderma, and probably others which are not often taken in a surface dredge and for that season were not detected). The deepest portions of the channel are populated by *Laminaria digitata* and *L. saccharina*. In the holdfasts of these algae are found aggregations of small animals which occupy this microhabitat. Sea squirts (Molgula, Botryllus); mat-forming bryozoans; developing sponge colonies (Chalina, etc.); small specimens of sea anemones (Metridium); the bivalve Saxicava; and seed of the blue mussel (Mytilus) are often attached within the ramifications of the holdfast. Small motile animals, such as Gammarus and other amphipods; isopods; the worms Lepidonotus and Nereis; crabs (Neopanope, small specimens of Cancer and Carcinides); small sea urchins (Strongylocentrotus); the brittle star (Ophiopholis); developing starfishes (Asterias); a flatworm (Leptoplana); periwinkles *(L. Littorea)*; and fish fry are found living within the holdfasts. Probably these are the most important microhabitats of the bottom community. On the stipe and fronds of the same algae are colonies of Sertularia, Tubularia, Obelia (hydroids), crustose bryozoans of various species, Lichenophora, Bugula (bryozoans), Ectocarpus (alga), Spirorbis (annelid), small amphipods, *Littorina littorea*, Lacuna (snails) and small specimens of Asterias. Laminaria produces important reactions by slowing the current of water, reducing light intensity, and serving to catch and hold sediment, as well as serving as a place for attachment or refuge for many animals. Andrews (1945) described the kelp bed communities of the Monterey Region of California and showed the importance of the large algae in determining the nature of the community.

Among the laminarian plants are other algae such as tufts of Chondrus, masses of Chaetomorpha, Euthora, and strings of Chorda. Chaetomorpha often harbors a number of the bivalve Gemma, shrimp (Crago), and the amphipod Caprella. Euthora is often crusted with a lacework of bryozoans and riddled with Caprella, Aeginina, Idothea and other crustaceans as well as immature annelids.

These colonies of algae with their associated animals do not form a solid mass of vegetation over the channel bottom, but occur in small groups, usually from one-half to four square feet in area, wherever anchorage of some kind is available. Laminaria is attached to rock outcrops, stones, shells, mussels, or any other solid object to which the plant can cling for support. Likewise for the other algae, except that less support is needed for them since many of them can secure a foot-hold in the sand, and once a nucleus is begun, other plants and animals adhere to it.

Colonies of Chalina (sponge) and Abietinaria (hydroid) are frequently attached to these islets of organisms and are also scattered about anchored in the sand. Chalina often harbors a number of animals which use the sponge for support, as, for example, Lepidonotus (annelid), seeds of bivalves, Caprella

(amphipod), and Ophiopholis (brittle star). Shallow muddy and sandy areas often swarm with the snail *Nassarius trivittata*, while shelly, rocky bottoms have many specimens of Metridium (sea anemone), *Crepidula fornicata* (boatshell), and to a lesser extent Acmaea and Anomia (mollusks). Along springlow-water line and somewhat below, there is found, attached to rocks, colonies of the rock seaweed *Fucus edentatus*.

On the whole, the benthos community is fairly uniform throughout the inlet with only minor differences at certain local areas where the substratum is somewhat different. The permeant influents (see list) are wide ranging and are found on all kinds of bottom. Very few species are restricted to any one of the four type bottoms, although often a greater abundance of some animal is found on one kind. Sumner, Osburn, & Cole (1913) concluded that the type of bottom was most important in explaining distribution of subtidal organisms. Thus 40% of the animal life dredged in Buzzards Bay (mud bottom) was not found in Vineyard Sound (sandy, gravelly bottom), while 35% of the latter was not found in the former. Verrill & Smith (1873) and Lee (1944) who studied in the same area also found correlations between the bottom organisms and the substratum. Shelford (1935), however, has pointed out that communities are often more closely related to physiographic forces than to bottom materials, and MacGinitie (1939) has reported different communities on similar habitats. Allee (1923, pt. 3) holds the common view that "if forced to make use of a single criterion to divide the communities of the Woods Hole littoral I should depend more on observation of the character of the sea-bottom than on any other one factor." The real influence of bottom material is apparently but little understood, although admittedly important (Petersen 1918).

The interrelationships among the major plants and animals were studied with particular reference to each individual community as a microcosm, and in the case of those of the intertidal region, to the influences of the fluctuating tidal level. These relationships are summarized in the form of food-chain diagrams which outline the most significant coactions which were found to be taking place in each community. No claim is made for completeness in this study, but rather the aim has been to determine the main lines of interactions which control the communities. In addition to the diagrams, there is a brief account which explains them.

The food habits of the fishes, birds, terrestrial arthropods, and some of the little-known marine invertebrates have been determined for the most part from published literature, although field observations were made to corroborate the findings recorded in publications. The major coactions of the marine organisms were observed at first-hand. Heavy lines in the diagrams indicate the most significant species and coactions of that community.

The interrelationships of the pelagic and subtidal communities of the shallow inlet cannot be very well

separated since the dynamics of one overlaps that of the other. For that reason the two are considered together. The coactions of these two biomes are probably much the same at all times throughout the aestival season of any one year with two important variations. First, the fish population changes in composition and abundance during the summer months, and secondly the concentration of the submerged fauna is increased during low-water when the permeant and other motile animals withdraw from the tidal zone and congregate in the narrow channel. At high-water these motile animals invade the shore zone in search of food and thus decrease the food-chain activities taking place in the subtidal region at that time.

The algae (Laminaria, Chaetomorpha, Ulva, Chondrus, etc.) of the river bottom are the basic foods for many snails (Littorina, Lacuna), crustaceans (Crago, Cancer, Pagurus, Carcinides, etc.), and fishes. The herbivorous snails are devoured by carnivorous ones (Polinices, *N. trivittata*) and both types are eaten by crabs and fishes. The smaller fishes are eaten by larger ones and also by the diving birds (terns, kingfishers).

Plankton and detritus are consumed by bivalve mollusks which are attached by the carnivorous snails, the horseshoe crab or kingcrab (Limulus), decapod crabs, starfishes (Asterias), annelids (Nereis), and bottom fishes (flounders, sculpins, skates, squirrel hake, etc.), the latter consuming also all of the invertebrate enemies of the bivalves. Plankton-feeding fishes (mackerel, herring, pollock, pipefish, etc.) are devoured by the predaceous ones (bluefish, butterfish, silver hake, etc.), or by diving birds. Coelenterates, sponges, and bryozoans feed on the plankton and detritus, and they are eaten by crustaceans and fishes. Annelid worms and shrimps feed on organic matter, or "marine humus" (Waksman 1933), in the bottom sands and muds and they are dug out and eaten by the kingcrab, rock, hermit, and green crabs and by bottom-living fishes. Dead animal bodies and other organic refuse are eaten by scavenging snails, crabs, amphipods, and fishes.

As it is readily seen, the food chain is founded in algae, organic debris with its bacteria, and plankton. Detritus with adhering bacteria is probably of great importance to those organisms feeding on microscopic materials (Blegvad 1914). The importance of bacteria in the food cycles of the sea has been shown by Waksman (1934) and ZoBell (1946). Mare (1942) has studied and diagrammed the food cycle of an English subtidal community and has shown the importance of microorganisms in the cycle. The major intermediate animals are gastropods, annelids, and crustaceans, which become food for fishes, some of which at least are preyed on by the harbor seal (Phoca) and some consumed by man. (Compare these levels with the system of Lindeman 1942.) Figure 4 outlines the main coactions taking place in the pelagic and subtidal region. Bond (1933) has called attention to the importance of particulate organic matter in aquatic food cycles and has suggested

the latter is probably most important for the zooplankton. Steven (1930) has pointed out that while some fishes are selective feeders, stomach content analysis indicates that most fishes eat whatever is available, and Shelford writes "each species selects the food available in greatest quantity, making selections which in a particular locality tend to give an erroneous impression as to the specific nature of food relations." In any particular community, however, the food chains are bound to be limited and more or less specific although it must be kept in mind that such a "web of life" is not the only such pattern found and will vary in each community according to its composition.
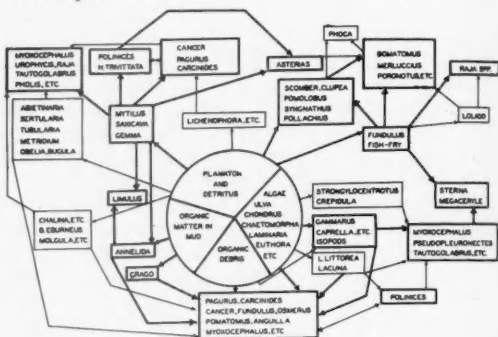
Fig. 4. Food coactions of the subtidal Laminaria-Cancer faciation.

Annuation and Succession

During the period of this study, a number of changes occurred in the marine biota of such a magnitude as to be easily detected by ordinary sampling and observation. Some of these changes can be explained by the influence of man, by disease, by extreme temperatures, by competition or predation, but for many we have no clue as to the cause. Some species increased while others decreased; some changes were extremely rapid while others were slow. Probably the operating forces in each case were different and each would have required a special study in itself, although undoubtedly many of them were related in one way or another. A study of the meteorological and hydroclimatic conditions at Cape Ann during the period of this study does not show any direct correlation between fluctuations of physical factors and the biota with the exception of the influence of low temperature on certain crabs mentioned hereafter. Moberg & Allen (1927) have shown that the properties of seawater near shore change suddenly and frequently, and only a complete and continuous analysis can detect such changes accurately. However, even without an adequate explanation, it is worth recording observed fluctuations of ecological significance. The sudden and voluminous increase in abundance of certain species which were formerly very scarce, such as a few of those recorded in this paper, raises a question as to the potential significance of some uncommon species generally overlooked by ecologists.

The eel-grass, *Zostera marina*, all but disappeared in 1932 as the result of an epidemic. During the first season of this field survey it was found persisting in a single brackish lagoon (Goose Cove). Even there it dwindled for several years. Each year after 1934 more and more patches were discovered in scattered locations of the inlet growing chiefly from old rhizomes, but in no case was a good healthy stand of this plant found until the summer of 1945. By that time, a sizeable stand had returned in Goose Cove (northeast of Station V), and to a lesser extent in the channel leading to it. These were extended considerably by the summer of 1946 but it has not yet returned in the region in sufficient quantity to be of ecological significance. Two crustaceans, the lobster *(Homarus americanus)* and a mud crab *(Neopanope* sp.), practically disappeared from the inlet with the eel-grass. How much influence can be attributed to the loss of the eel-grass cannot be stated. Both crustaceans returned in small, but in increasing numbers, after 1936. A snail, *Lacuna vincta*, formerly found on the eel-grass, moved to the brown algae *Laminaria digitata* and *L. saccarhina* when the eel-grass disappeared. This snail remained a common species until 1935, when it became very scarce for two years. In 1937 it began to return in larger numbers and was still increasing in 1940. Stauffer (1937) found that animals formerly found on eel-grass in the Woods Hole region either adapted themselves to living on the mud or disappeared.

Another snail, *Polinices heros*, on the other hand, increased in abundance each year from a small population in 1933 to a very large one by 1937. One factor concerned in this increase was the virtual elimination of the green crab, *Carcinides maenas*, which was dredged from the channel and destroyed in its hiding places on shores and marshes by the Massachusetts Bureau of Marine Fisheries in the winter of 1933-34. The severe weather of that season (as low as −20° F.) is also believed responsible for killing a large number of the crabs while wintering in the marshes. This crab was not found in significant numbers again until 1936 when it was once more reduced in abundance by the Bureau of Marine Fisheries. Allee (1919, 1923 pt. 4.) determined changes in the Woods Hole fauna after a severe winter and discussed the importance of temperature in relation to annuation. Blegvad (1929) and Caullery (1929) also described changes in abundance of marine organisms as a result of a very severe winter season.

During the absence of the green crab, the rock crab, *Cancer irroratus*, was noticeably more abundant. The common starfish, *Asterias vulgaris*, suddenly became much more abundant in 1935 than it had been previously. Dredge hauls that year from the northern channel averaged 33 specimens. This increased population was maintained, but not at such a high level, for the next two years. Galtsoff & Loosanoff (1939) found that increases in population of *A. forbesi* were caused by increased rates of reproduction and survival rather than by invasion. Burkenroad (1946) has demonstrated a 14-year cycle of abundance of

this same species. *Limulus polyphemus* and *Lepidonotus squamatus* were not collected in their usual abundance in 1935.

The most important change which has taken place each year in the inlet is the annual deposition of silt and sand. This has led to the formation and extension of bars, flats, and beaches. The Annisquam River originally had a natural depth of about 6 feet at mean-low-water from Ipswich Bay to Little River, while from this point to where the railroad bridge now crosses Station E it gradually decreased in depth. Beyond, the channel was reduced to a drainage ditch, the bottom of which ranged up to 2 feet above mean-low-water level. The inlet was terminated at this point by the land bridge or bar previously discussed. The canal through the bar and the natural inlet (Annisquam River) have been dredged from time to time to widen and straighten the channel for passage of the larger fishing vessels, as it occupies the accumulated deposits which have tended to obliterate the inlet, and which indeed nearly succeeded in doing so before white man appeared on the Massachusetts coast. At intervals between 1906 and 1929 the Commonwealth of Massachusetts dredged various sections of the inlet to a depth of 8 feet at mean-low-water. The last dredging in this series was completed in September of 1929 when 50,428 cubic yards of material were removed, four years before this ecological survey was begun. In 1936 the Federal Government restored the channel to its 8 foot depth and straightened and widened it in places by removing 91,773 cubic yards of bottom deposits.

As the bars and flats are rebuilt, the subtidal bottom community becomes more and more restricted, and through this process of physiographic succession becomes replaced by the intertidal communities of sediments—chiefly the Mya-Nereis pelagica Biome.

TIDAL COMMUNITIES OF SEDIMENTS

MYA-NEREIS PELAGICA BIOME

General Character

This bivalve-annelid community resembles that of the Mya-Nereis virens Biome described by Newcombe (1935). At Cape Ann the dominating annelid is of a different species. This community is probably very extensive along the New England coast, as it occupies most of the periodically exposed bars and flats of all kinds of loose sediments from about mean-low-water line to a vertical height of about 4 feet. Like that described by Newcombe (1935) this community does not descend into the subtidal region.

In the listings of the predominants of intertidal communities, the first number given is the average abundance on 400 square inches of the samples of that species taken from all levels in a particular community. The second number is the percentage of occurrence of that species in all samples taken in that community. Thus, *Mya arenaria*, soft-shell clam, 22/46 indicates that this bivalve had an average abundance of 22 specimens on 400 square inches, and that this species was found in 46 per cent of all

quadrat samples taken in the Mya-Nereis pelagica Biome of the Annisquam inlet.

Dominants and Slow-Moving Influents
Dominants

Mya arenaria, soft-shell clam, 22/46

Nereis pelagica, clam worm, 16/45

Lumbrinereis tenuis, annelid, 52/50

Clymenella torquata, annelid, 609/19

Subdominants

Macoma balthica, bivalve, 6/24

Polinices heros, sand-collar snail, 1/9 (at low-water)

Influents

Glycera dibranchiata, annelid, 3/19

Gammarus locusta, amphipod, 154/6

Nassarius obsoletus, snail, 40/4

Talorchestia longicornis, amphipod, 6/14

Chaetomorpha linum, green alga, Com./15

Subinfluents

Solemya velum, bivalve, 4/13

Gemma gemma, bivalve, 51/23

Ensis directus, razor clam, 2/5

Cerebratulus lacteus, nemertean, 2/4

Onoba aculeus, snail, 61/21

Littorina littorea, periwinkle, 21/22

Anurida maritima, insect, 78/8

Ulva lactuca, sea lettuce, Num/15

Permeant Influents

Pagurus longicarpus, hermit crab

P. pollicaris, hermit crab

Cancer irroratus, rock crab

Carcinides maenas, green crab

Limulus polyphemus, horse-shoe crab

Crago septemspinosus, shrimp

Fundulus heteroclitus, minnow

Tautogolabrus adspersus, cunner

Myoxocephalus octodecemspinosus, long-horn sculpin

Pseudopleuronectes americanus, cunner

Larus argentatus, herring gull

Pisobia minutilla, least sandpiper

Ereunetes pusillus, semipalmated sandpiper

Charadrius semipalmatus, semipalmated plover

Actitis macularia, spotted sandpiper

Butorides virescens, green heron

Nycticorax nycticorax, black-crowned night heron

Corvus brachyrhynchos, crow

Secondary Forms

Mytilus edulis (seed), blue mussel, 15/9

Dolichoglossus kowalevski, acorn worm, 9/7

Balanus balanoides, barnacle, 45/3

Littorina saxatilis, snail, 29/5

Allorchestes sp., amphipod, 18/1

Mulinia sp., bivalve, 1/3

Asterias vulgaris, starfish, 1/1

Siliqua costata, sand-bar clam, 2/1

Enoplobranchus sanguineus, annelid, 2/1

Idothea baltica, isopod, 2/1

Cyathura carinata, isopod, /1

Faciations

Two faciations are recognized at Cape Ann as an expression of bottom effect. The Talorchestia Faciation occupies the coarse sediments (sand bars, beaches) and might be considered as a skeleton Mya-Nereis pelagica Community composed almost entirely of the dominants with a few additions, such as the characteristic sand-dwelling amphipods. The Macoma-Clymenella Faciation of the mud flats, in addition to the dominants of the biome, has many other species, and a much greater abundance of life than is found in the other faciation. This is probably explained by the fact that the silt and clay deposits contain a much higher concentration of organic detritus with favorable conditions for microorganisms, and they have a smooth, moist surface which is favorable for many motile animals. Stephen (1928, 1929, 1932-34) has studied quantitatively the bivalve-annelid communities at many points along the Scottish coast. He recognized the Tellina tenuis-Nephthys caeca Association on clean sand, the Cardium edule-Macoma balthica Association on black mud, and transitions between the two. He also determined the zonation of the predominants in each case.

Some bars and flats are composed of a mixture of sand and mud in various degrees, and here will be found a mixture of some of the animals which ordinarily prefer one or the other type of substratum and a rough correlation in abundance according to the proportion of the mixture. Bruce (1928), Pirrie, Bruce & Moore (1932), and Newcombe (1935) have all shown the importance of the texture and size of particles of sediment and their influence on the distribution of certain animals.

Fragments of another community (Balanus-Mytilus-Ascophyllum Association) occur wherever rocks or other hard surfaces are present. These spotted fragments give rise to a condition which might be compared to the savannah type of community on land (Newcombe 1935 and Shelford et al. 1935). To the rocks are attached *Balanus balanoides* over most of the exposed surface. *Fucus vesiculosus* is often draped over much of the surface, and *Mytilus edulis* is attached around the base of the rocks and in crevices. On the barnacles and mussels are Asterias and Thais, while on the Fucus are *Littorina littorea*, *L. obtusata*, Sertularia, and Clava. Small rocks and shells on the mud attract *L. littorea* and *L. saxatilis* into concentrated groups.

Zonation and Coactions

The communities are first described as they are organized at the time of spring-low-water. Changes in composition and the resulting interactions brought about by the incoming tide will be explained as the water level gradually rises. This plan will be followed throughout the description of the intertidal communities.

Between the lowest water level reached during the spring tides and the mean-low-water line is a transition zone which might be considered an ecotone. It contains organisms of both the subtidal and intertidal regions. Lepidonotus (annelid), Aeolis, Onchidoris (nudibranchs) are found under small stones while *Nassarius trivittata* (snail), Mulinia, Siliqua (bivalves), Strongylocentrotus and Echinarachnius (echinoderms) are occasionally found on or in the sand along this lowest zone where they have been exposed by the extreme low tide. Lumbrinereis, Clymenella, Nereis, Glycera (annelids), Ensis, and Solemya (bivalves) of the intertidal group penetrate

to this level and intermingle with the fringes of the subtidal community. Clymenella is generally restricted to the lower part of the shore and the greatest concentration of Glycera and Solemya is also found there.

Ensis extends back to about midpoint on the shore. Lumbrinereis and Nereis range back to the highest point on the bars, and for a considerable distance up the beaches, declining in abundance toward the higher portions of the strand. The distribution of Mya (clam) begins several inches above spring-low-water line and extends to the top of bars and to the level of the marshland on the beaches and flats. Macoma has much the same limits but is found in smaller numbers. Gemma is often spotted over the entire bar or flat, but reaches greatest concentration under and among the fronds of Chaetomorpha which often coat large areas of the flats, after being dropped there by a retreating tide. On some shores *Littorina littorea* may be found at any level, especially around pebbles or fragments of seaweed cast upon the beach. Polinices also is located at all levels on the sandy bars and beaches. Usually this snail moves off the tidal zone with the retreating tide, but when exposed on the shore it buries itself below the surface. It can then be detected by a low mound of sand directly over it. Talorchestia (amphipod) might be found anywhere from the middle to the highest point of the shore, but it is generally in greatest numbers along the highest level. The same distribution of this crustacean was noted by Davenport (1903).

This typical community as just described is found on the sandy bars and wet, firm, sandy beaches. A broad beach such as Wingersheek Beach at Station W (Table 4, Fig. 5) extending as it does to spring-high-water line, has a high margin of dry, clean sand which is not very densely populated by plants or animals. The composition of the community is much the same, but the concentration of organisms is not as great, especially in the high, dry sand. Marsh communities are gradually invading this area, with pioneer low marsh and high marsh organisms already present over a considerable portion of the upper level at one end of the beach. The Talorchestia Faciation was studied at Stations A, S, and W, with a total of 84 quadrat counts.

The Macoma-Clymenella Faciation was studied at stations D, F, I, J, N, O, Q, while a mictium of the two was found at station G (Table 5). One hundred and five quadrat counts were made in all. Additional members of the mud flat assemblage not found in or on the sand included the following: *Nassarius obsoletus* was found in varying quantities on the flats, being most abundant on the soft, black muds which had a jelly-like consistency, and which were protected in small bays and inlets. It extended from low-water level to the junction of the flats with *Spartina glabra* marshland. Cerebratulus was centered chiefly in the lower portion of the shore while Dolichoglossus centered in the middle of the shore. Talorchestia was not found on the muddy shore, while no case was found where the exposed flats

TABLE 4. Station W. Sandy beach. Top number sample of 7-23-35; bottom number sample of 7-23-36. Key to Tables 4 to 10 That Show Composition and Zonation of Intertidal Communities.

Each column represents a quadrat level. Distances between quadrats are recorded as follows: D = number of feet down-shore measured along the ground; L = number of inches lower measured vertically. Numbers indicate abundance on 400 square inches. Each group of numbers gives the abundance for each year reported. Abun. = abundant; Com. = common; Num. = numerous; Sm. Amt. = small amount; S = seed or juvenile individuals. In those tables in which more than one community is represented, each community is separated by double vertical lines.

Only a few of the stations studied by quadrat sampling are represented by the selected tables presented in this paper and in some cases not all quadrat counts taken at the stations included here are listed. No one station and no one series of samples may be regarded as typical of the community composition and organization as described in the text. The evaluations and descriptions are based upon an over-all study of all of the shores and samples taken over a period of five years.

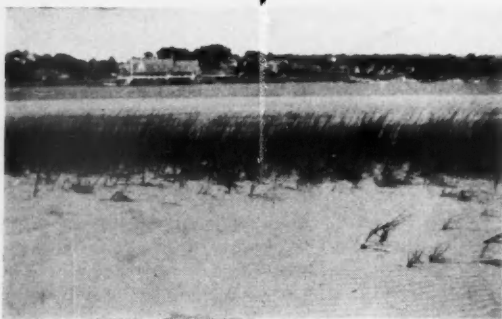|	1 Near M.H.W.L.	2 20D; 8L	3 40D; 8L	4 20D; 6L	5 26D; 5.5L	6 26D; 4L	7 26D; 3.5L	8 26D; 2.5L	9 26D; 3L	10 26D; 1L	11 26D; 12.5L	12 26D; 6.5L	13 26D; 4L	14 26D; 6L	15 26D; 6L	16 26D; 6L	17 26D; 4.5L
Orchestia platensis	400 4																
Terrestrial arthropods	4 0	0 8	1 0		2 0	8 0	3 0										
Talorchestia longicornis	0 4	0 8	7 20	1 0				1 0			5 12	2 0	2 0			0 2	
Littorina littorea		0 4			2 2	2 60	1 12	0 2	0 2								
Littorina saxatilis		0 1		2 4	1 28	1 28	0 16		0 6	0 92							
Spartina patens			Com. Com.														
Spartina glabra					Com. Com.					Com. Com.							
Mat of algae					Abun. Abun.	Com. Sm. Amt.	0 Sm. Amt.	0 Sm. Amt.									
Nereis pelagica						0 2					0 2			0 2			
Mya arenaria						0 2	3 6	2 16	1 8		0 10	7 8	5 4	10 8	12 4	9 0	
Lumbrinereis tenuis															0 4		30 12

FIG. 5. Sandy beach at station W occupied by the Talorchestia faciation of the Mya-Nereis pelagica biome. Notice invasion of marsh grasses on higher beach level.

reach a level high enough to have a deposit of sea-wrack with its attendent fauna of Orchestia and its associates, as was found on the sandy beaches. Cerebratulus, Clymenella, Gammarus, Dolichoglossus, Anurida, *L. littorea*, Ensis, and Solemya were much more numerous in this faciation, while some others were practically restricted to it (Nassarius, Onoba, and a number of less significant species). Table 6 and Figure 6 portray typical mud flat conditions at Cape Ann. Verrill & Smith (1873) described animal communities in the mud and sand sediments of the intertidal region of Vineyard Sound. Appellöf in Murray & Hjort (1912) described similar communities for various sections of the Atlantic coast. The papers of Allee (1923) include collecting records from sediments of the Woods Hole region analyzed from a community point of view. Pearse, Humm, and Wharton (1942) studied in detail the inhabitants of the sand beaches at Beaufort, N. C. In the British Isles studies on communities of marine sediments have been made by Bassindale (1938), Beanland (1940), C. B. Rees (1940), Spooner and Moore (1940), and Brady (1943).

During low-tide there is a minimum of activity. The marine invertebrates which remain on the ex-posed shore cease movement almost entirely, and what feeding activities take place are, for the most part, those of land animals, particularly birds, which feed on the exposed shores. *L. littorea* and Onoba continue to feed to some extent on Ulva, Chaetomorpha, Laminaria, etc., which have been washed ashore, and on microscopic algae on the shore, although for the most part they remain idle at this time. Haseman (1911) found there was no rhythm in the movements of *L. littorea* in the absence of a tidal flow, and the writer has found that often a number of specimens will continue activities even though exposed. Stranded starfishes (Asterias) are not very active, but do feed on the tiny bivalve, Gemma, which they can easily pick up from the surface. Anurida (insect) is the exceptional surface invertebrate which is at its peak of activity at this time, hunting dead bodies of fishes, mollusks, crustaceans, etc. on which it feeds. A special report on the scavenging activities of this marine insect has been published earlier (Dexter 1943c). *Nassarius obsoletus* and Gammarus also are somewhat active if a carcass is near at hand or if the substratum is moist and smooth. In the sand or mud, activity is normal. Nereis, Glycera, and other carnivorous annelids feed on the bivalves. Clymenella, Lumbrinereis, etc. feed on the bacteria (MacGinitie 1932, 1935) and organic matter in the mud, while Polinices bores into the bivalves.

The shore birds, herons, gulls, and crows use the uncovered shoreline for a hunting ground. They feed on annelids, snails, bivalves, crustaceans, starfishes, and debris. This is essentially the same as the food chain reported by MacGinitie (1935) for Elkhorn Slough: "Plants → Detritus and bacteria → Detritus feeders → Animal feeders → Birds." ZoBell & Feltham (1942) have shown the importance of bacteria in the food cycle of such mud flat communities.

As the tide returns, the bivalves of the lower beach, Ensis, Solemya, Gemma, and Siliqua, extend their siphons and again strain the water of its plankton

TABLE 5. Station G. Sandy-mud bar. Top number sample of 7-4-35, middle number sample of 7-4-36, bottom number sample of 7-5-37. The dominants only are shown. Legend as on Table 4.

	1 Near top of bar	2 40D;7L	3 30D;5L	4 22D;7L	5 22D;5L	6 22D;10.5L
Mya arenaria	20;368S 60;88S 0	160;420S 36;136S 8	200;744S 32;72S 104;412S	32;488S 12 108;388S	12 4 48;812S	1 0 56;676S
Nereis pelagica	18 8 24	17 0 12	17 12 4	14 16 0	27 24 0	5 8 4
Macoma balthica	5 0 0	6 8 0	10 4 4	1 0 4	....	0 0 8
Clymenella torquata	0 0 4	....	....	....	600 0 0	1200 0 0

TABLE 6. Station Q. High marsh, low marsh, and mud flat. Top number sample of 7-13-35, bottom number sample of 7-13-36. Legend as on Table 4.

	1 Near M.H.W.L.	2 12D;35.5L	3 12D;22L	4 40D;8.5L	5 26D;5.5L	6 16D;3L	7 16D;6.5L
Spartina patens.........	Abun. Abun.						
Orchestia platensis.......	0 68						
Anurida maritima.......	25 0	25 40					
Littorina saxatilis.......	1 4	0 16					
Littorina littorea........	42 112	96 296	3 100	1 0			
Spartina glabra.........	....	Abun. Com.					
Fucus vesiculosis........	....	Com. 0					
Balanus balanoides......	....	2000 0					
Littorina obtusata.......	....	8 0					
Mytilus edulis..........	....	1 1	50 0				
Lumbrinereis tenuis......	....	....	20 0	60 16	24 0		
Nereis pelagica..........	....	....	8 0	12 12	13 0	6 24	0 4
Mya arenaria...........	....	....	20;140S 20;40S	3;788S 100;360S	2;580S 4	512S 8 S	5S 0
Macoma balthica........	....	....	20 4	44 12	10 4	6 0	1 0
Glycera dibranchiata.....	....	....	1 0	....	1 0	1 4	4 12
Clymenella torquata......	....	....	....	0 48	12 400	12 800	3600 1200
Solemya velum..........	....	....	....	1 0	....	....	1 2
Polinices heros..........	....	....	....	....	1 0		
Chaetomorpha linum.....	....	....	....	....	....	0 Sm.Amt.	
Onoba aculeus..........	....	....	....	....	....	0 4	
Gemma gemma..........	....	....	....	....	....	0 24	
Cerebratulus lacteus......	....	....	....	....	....	2 0	0 2

FIG. 6. Mud flat at station N occupied by the Macoma-Clymenella faciation of the Mya-Nereis pelagica biome.

FIG. 7. Food coactions of the Mya-Nereis pelagica biome of intertidal sediments.

and bacteria-laden detritus. As the water level rises and reaches other bivalves (Mya, Macoma), they do likewise. The inflowing waters give the annelids and nemerteans an opportunity to escape and swim off to another location. With the advance of the water, the birds are gradually forced back until they are no longer able to feed on the shore. Replacing the shore birds is a constant stream of shrimps (Crago), minnows (Fundulus), and crabs (Carcinides, Cancer, Pagurus) which come upon the shore as rapidly as the water advances and feed upon the worms (Nereis, Glycera, Lumbrinereis, Cerebratulus, Clymenella), snails (*L. littorea*, Onoba, Nassarius), and bivalves (Gemma, Ensis, Solemya, Mya, Macoma), as well as upon organic debris. As the water deepens, bottom fishes (flounders, sculpins, skates), kingcrabs (Limulus), sand-collar snails (Polinices), and starfishes (Asterias) invade the shore to feed on the worms and mollusks.

When the water floats the stranded masses of Chaetomorpha, the animals *L. littorea*, Onoba, Caprella, and Gammarus become more active in their feeding and locomotion. Anurida retreats up the shore. hides in air bubbles in the mud, or is floated upon the incoming water. By the time the tide has come in three feet above spring-low-water-line, all of the communities inhabiting the bars have been covered, and with an additional foot of water all of the communities inhabiting the mud flats and sandy beaches (except at Station W) have been inundated. These rhythms of activity are associated with rhythms of oxygen consumption by the tidal invertebrates, being greatest during submergence (Gompel 1938). See Figure 7 for diagrams of food coactions of this community at low tide and at high tide.

Annuation and Succession

Mya arenaria was declining in abundance seriously at the beginning of this study. Over-taking of clams by the clam industry, natural enemies, covering of the flats by blue mussels, and the absence of eel-grass to hold the clam seed were causes contributing to the decline. In 1934, the Massachusetts Bureau of Marine Fisheries planted hundreds of bushels of clam seed in flats north of Cape Ann, and without doubt
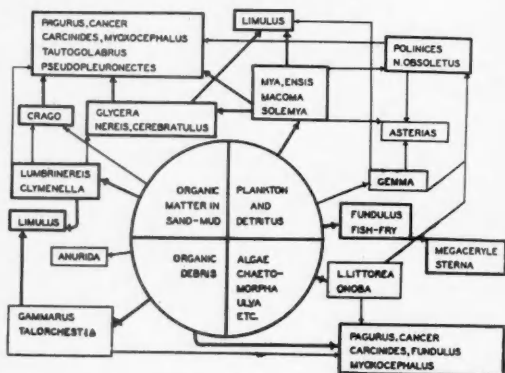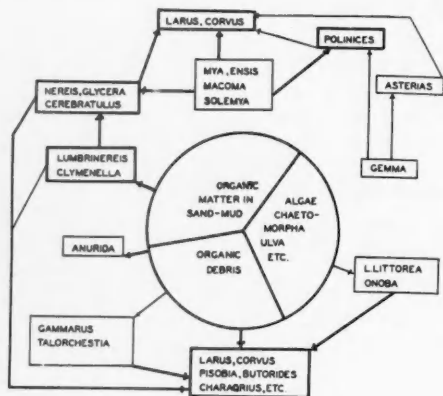
some of the spawn drifted into the Annisquam inlet. In the absence of *Carcinides maenas*, mentioned earlier, and with the removal of blue mussels from many of the flats, a good set of clam seed was established. Natural reseeding also played some part in this reestablishment. Between 1936 and 1937, the Bureau of Marine Fisheries placed 400 bushels of seed clams into the flats of the Annisquam waterway. By 1940, *Mya arenaria* was again a very common species, although for the most part still small in size. Newcombe (1935, 1936) observed annual fluctuations in soft-shell clam populations in the Bay of Fundy region and has shown that the rate of growth during the first four years of life is rapid for this species.

Nereis pelagica increased in abundance in 1934, maintained its numbers until 1936, when it declined to about the 1933 level. It then decreased still further the following season. *Nereis virens* was collected in 1932, the season preceding the beginning of this survey, but was never found again in subsequent years. *Lumbrinereis tenuis* was not found in the same abundance in 1936 as in other years. *Clymenella torquata* increased during the first two years, decreased in 1936, and remained about the same the

following year. Phyllodoce catenula was collected during the summer of 1933 only. *Macoma balthica* increased for two years while *Mya arenaria* was decreasing, and then decreased while Mya was being reestablished. *Ensis directus* was found in less abundance each year, declining from a common species to one collected only rarely. *Nassarius obsoletus*, on the other hand, was collected in greater quantity each year after 1933 and extended its range considerably over the flats and marsh channels of the inlet. *Onoba aculeus* was less abundant in 1937 than previously.

As the accumulation of sediments continues, the bars and flats are extended and elevated with a resulting expansion of the Mya-Nereis pelagica Biome. Soon, however, the blue mussel *Mytilus edulis* begins to cover the sediments. At first this bivalve becomes attached to small rocks or shells lying on the surface. As clumps of mussels develop they attach to each other and eventually form a solid carpet over the bars and flats. By blanketing out the inhabitants of the sediments and providing a solid surface for attachment of other organisms, a new community comes into existence—the Balanus-Mytilus Faciation. At the higher level of the flats and beaches, within five feet of mean-high-water line, the thatch grass *Spartina glabra* invades the sediments as they are elevated to that level and extend the low marsh community (Spartina glabra-Littorina saxatilis—Brachidontes Associes).

TIDAL COMMUNITIES OF HARD SURFACES
BALANUS-MYTILUS-LITTORINA BIOME

General Character

The Balanus-Mytilus-Littorina Biome (barnacle-mollusk) is represented along the inlet by fragments of two faciations: Balanus-Mytilus and Balanus-Littorina-Ascophyllum Faciations. Together they form the communities on hard surfaces, particularly on rocks and over flats and beaches where they themselves produce a solid foundation. This biome is similar to the one described by Newcombe (1935) as Balanus-Littorina-Fucus, but here two separate faciations are recognized, and Mytilus is believed to be of greater significance than Fucus. This community is flooded and uncovered twice daily through a mean vertical height of 8.6 feet.

Studies on hard surface communities, particularly those of rocky shores, have been published by Verrill & Smith (1873), King & Russell (1909), Pearse (1913), Huntsman (1918), Allee (1923), Shelford & Towler (1925), Fischer (1928, 1929), Shelford (1930, 1935), Coleman (1933, 1940), Newcombe (1935a), Kitching (1935), Hewatt (1937), and T. K. Rees (1939).

Dominants and Slow-Moving Influents
Dominants
Balanus balanoides, rock barnacle, 740/81
Mytilus edulis, blue mussel, 72/60
Littorina littorea, periwinkle, 111/85
Ascophyllum nodosum, rock seaweed, Abun./47

Subdominant
Fucus vesiculosus, rock seaweed, Com./16
Influents
Littorina obtusata, seaweed snail, 51/47
L. saxatilis, snail, 77/34
Gammarus locusta, amphipod, 15/17
Thais lapillus, rock snail, 13/32
Asterias vulgaris, starfish, 2/11
Subinfluents
Anurida maritima, insect, 155/56
Orchestia platensis, amphipod, 41/11
Spirorbis spirorbis, annelid, 324/4
Neopanope sp., crab
Fucellia sp., seaweed fly
Coelopa frigida, seaweed fly
Permeant Influents
Carcinides maenas, green crab
Cancer irroratus, rock crab
Pagurus longicarpus, hermit crab
P. pollicaris, hermit crab
Tautogolabrus adspersus, cunner
Myoxocephalus octodecemspinosus, sculpin
Fundulus heteroclitus, minnow
Larus argentatus, herring gull
Corvus brachyrhynchos, crow
Secondary Forms
Acmaea testudinalis, limpet, 6/2
Crepidula fornicata, boat shell, 4/1
Obelia spp., hydroids, Com./11
Metridium dianthus, sea anemone, 3/7
Sertularia pumila, hydroid, Abun./3
Gemellaria loricata, bryozoan, Com./3
Schizoporella unicornis, bryozoan, Com./3
Tubularia spectabilis, hydroid, Com./1
Clava leptostyla, hydroid, 16/1
Fucus edentatus, kelp

Faciations

The Balanus-Mytilus Faciation (barnacle-mussel) develops on all kinds of bottom material—sand, mud, and rock. Mytilus forms extensive beds from spring-low-water line to a height of about 5 feet. Below the lowest tidal level the mussels are found in small groups only. Newcombe (1935a) found that while the growth of *M. edulis* in complete submergence is equal to that on the intertidal region, it was not present in the subtidal area of New Brunswick because of echinoderm predators, although it was present on the subtidal shores of Nova Scotia. Warren (1936) found the growth of *M. edulis* better when submerged, but again found the mussels absent below the low-water line in Passamaquoddy Bay because of predation. Without doubt the same factor is responsible for the smaller population of the blue mussels in the subtidal community of the Annisquam inlet. Above the 5 foot vertical limit of solid beds they are likewise scattered, usually small, and few in number. Seldom do they live for long because of the extended period of exposure. Upon the mussels are attached *Balanus balanoides* (rock barnacles), and upon these dominants as a substratum are found the other predominants.

The Balanus-Littorina-Ascophyllum Faciation (barnacle-snail-rock seaweed) is found on hard surfaces. Balanus and Ascophyllum attach to flat surfaces,

while Mytilus occurs in crevices and among the rocks. Over all is *Littorina littorea*, the most universally distributed organism in the marine communities of Cape Ann.

Zonation and Coactions

Balanus-Mytilus Faciation

Along the lowest margin of the mussel beds, at about spring-low-water line and somewhat above, there is an ecotone consisting of many sedentary animals which cling to the mussels for support. Sponges, hydroids (Tubularia, Obelia), bryozoans (Celaria, Electra, Lichenophora), sea anemones (Metridium) and the ivory barnacle *(Balanus eburneus)* are somewhat common, although spotted in distribution. In favorable locations they form a carpet over the mussels, but often are scarce or entirely absent. Beneath the railroad trestle at Station E a protection is afforded which makes possible a very abundant, sedentary fauna; but on the margin of the exposed beds these animals are less frequent. Among the mussels at this level are occasional specimens of Cancer, Carcinides, Pagurus, and Asterias waiting the return of the tide.

Scattered over the shore at any point, but more often along the lower portion, fragments of algae are found. Ulva, Chaetomorpha, Ascophyllum, Fucus are often left strewn about by the receding tide and on some beds Fucus grows attached to the shells. The mussel bed is a solid mass of the bivalve *Mytilus edulis* (including the var. *pellucidus*) firmly held together by byssal threads. It extends from spring-low-water line to the top of the bars and to within 4 or 5 feet of the spring-high-water line along the strand. *Littorina littorea* is numerous all over the beds while much of the exposed surface of the bivalves is coated with the rock barnacle *(Balanus balanoides)* from about mean-low-water line to the upper limit of the mussels. *Anurida maritima* is common along the upper half of the beds.

During exposure, activity is reduced to a small amount of feeding on algae by *Littorina littorea*, on barnacles and mussels by *Thais lapillus* (rock snail), and to the scavenging activities of *Anurida maritima*, the herring gull, and crow. The scavengers feed on dead animals that have been exposed or washed in upon the beds.

Beginning again at the spring-low-water level, the incoming water allows the sponges, hydroid colonies, anemones, and ivory barnacles to feed on the microscopic organisms and bacteria-laden detritus. As the water continually rises, the mussels open their shells tier after tier and resume the straining of water. From the mean-low-water line to the top of the bed, or to the highest level reached by the water if rocks continue above the bed, the rock barnacles *(Balanus balanoides)* likewise resume their feeding activity. *Littorina littorea* and *Thais lapillus*, when present, continue their wandering and feeding after being stationary since exposure. Thais was found to feed largely on Mytilus, but also to some extent on Balanus. Fischer-Piette (1934) reported observations

to the contrary. In some instances the writer found that both organisms were being attacked rather equally, but on the whole more borings were found taking place in *Mytilus edulis*. Newcombe (1935, and personal communication) claims that *L. littorea* also feeds on *B. balanoides*, although the writer failed to corroborate this after careful and extended observations in the field. The evidence seems to rest chiefly on the destruction of barnacle seed by *L. littorea*, probably incidentally as it scrapes off algae from hard surfaces. In any case, such a coaction could not be demonstrated on these shores to justify listing it as an item of importance. *Asterias vulgaris* invades the beds to open the mussels and barnacles, and fishes and crabs invade to scavenge about. *Anurida maritima* is forced off the shore again, and the birds take leave. The Balanus-Mytilus Faciation was found at Stations C, E, and V (Table 7, Figure 8). Thirty-eight quadrat counts were made.

Balanus-Littorina-Ascophyllum Faciation

Along the lowest zone of the rocky shores laid bare by the spring tides is an ecotone, which is found best developed at Station B (Table 8, Figure 9) at the junction of the inlet with Gloucester Harbor. There the rocks are exposed to the spring-low-water line while along the inlet the lower levels of the rocky shores are for the most part covered with sediments. *Chondrus crispus* is the dominant alga, with scattered tufts of *Ulva lactuca*. Spirorbis (annelid) and bryozoans (Gemellaria, Schizoporella) encrust many of the rocks. Crepidula, Acmaea, *L. littorea* (snails), and Asterias (starfish) constitute the motile animals, but they remain stationary during exposure. Wilson (1929) has called attention to the fact that *L. littorea* fastens itself to the rocks with a mucus secretion and withdraws into its shell.

Over the shore from mean-low-water line to about mean-high-water line are strewn masses of *Ascophyllum nodosum* and to a lesser extent *Fucus vesiculosus*. Coating nearly all hard, exposed surfaces are the barnacles, *Balanus balanoides*, and dotting the rocks and seaweeds are the periwinkles, *Littorina littorea*. On the algae in large numbers is the seaweed snail, *L. obtusata*, which is practically restricted to such a habitat. Mytilus often forms a floor between the rocks and fills most of the crevices in them, especially around their bases. Crawling over all—rocks, barnacles, mussels, seaweed—is the ubiquitous insect *Anurida maritima*.

Thais (rock snail) occupies the lower third of the shore on the barnacles and mussels. In this zone Gammarus (amphipod) is most numerous, living under the seaweed (often in pairs); and Sertularia and Clava are attached to the algae in large colonies. Asterias at times remains on the exposed shore. Acmaea and *Crepidula fornicata* (snails) are rarely present.

Carcinides is common, hiding under seaweed and in crevices during the exposure of the shore, while Neopanope and occasionally Cancer (crabs) hide beneath loose rocks and bunches of seaweeds. All of

TABLE 7. Station E. Mussel bed. Top number sample of 8-16-35, bottom number sample of 8-12-36. Legend as on Table 4.

	1 Base of seawall	2 16D;28.5L	3 36D;13.5L	4 36D;17.5L	5 4D;5L	6 2D;10L	7 2D;10L
Anurida maritima	0 24		0 32				
Balanus balanoides	4000 2400	800 40	1000 20	200 4	160 20	80 0	40 —
Littorina littorea	72 56	72 28	120 24	60 56	20 12	4 0	16 —
Mytilus edulis		80;2000S 16;740S	1200 16;660S	200 24;340S	100 24;240S	96 28	32 —
Nassarius trivittata				0 6			
Obelia sp.				Com. Num.	Abun. Num.	Abun. Abun.	Sm.Amt. —
Asterias vulgaris				1 1	1 6		1 —
Metridium dianthus				0 1	0 4	4 4;128S	4 —
Cancer irroratus				0 1	1 2	0 6	1 —
Balanus eburneus						25 0	
Chondrus crispus							6 —
Sponge							50 sq.in. —
Tubularia spectabilis							25 —

FIG. 8. Mussel bed at station V. The Balanus-Mytilus faciation has developed over sediments. Notice the invasion of low marsh on the highest level of the mussel bed.

these are commonly found paired during the latter part of the summer and remain paired even when disturbed.

Over the upper half of the shore *Littorina saxatilis* is common, especially among the smaller, loose rocks, around mean-high-water line. Orchestia (amphipod) is often abundant among the algae, and at times Tabanus, Culicoides, and other flies take refuge there. The highest reaches of the community consist chiefly of *Balanus balanoides, Littorina saxatilis, L. littorea,* and *Anurida maritima.* The vertical distribution of the three species of Littorina is believed to be correlated with the varying resistance of these species to adverse conditions (Gowenlock & Hayes 1926). Some of the larger groups of rocks near high-water-line and above are used by the herring gulls for dropping hard shelled animals to break them open prior to eating the soft parts. On certain rocks regularly used for that purpose shell heaps accumulate (Dexter 1943b).

Not all of these communities occupy the full breadth of the intertidal zone; but where they are found they contain the species characteristic of that level. The Balanus-Mytilus-Ascophyllum Faciation was studied at Stations B, H, K, M, P, R, T, and X, with a total of 141 quadrat counts (Tables 8, 9; Figs. 9-12).

TABLE 8. Station B. Rocky shore. Top number sample of 9-3-35; bottom number sample of 9-7-36. Quadrat No. 10 for 1936 only. Legend as on Table 4.

	1 Gravel bank	2 30D;42L	3 20D;4L	4 50D;6.5L	5 21D;0L	6 21D;3.5L	7 21D;6.5L	8 15D;7L	9 15D;4L	10 15D;6L
Anurida maritima	1 4	20 56	0 24							
Littorina saxatilis	1 0	....	112 0	48 0	....	16 0				
L. littorea	1 0	40 16	900 432	640 128	244 376	100 56	124 100	272 480	180 340	— 144
Balanus balanoides	......	8 4	800 108	520 28	720 20	3600 800	40 28			
L. obtusata	......	0 8	......	0 60	200 32	24 40	96 64	44 100	16 8	
Cancer irroratus	......	......	0 1							
Fucus vesiculosis	......	4 0	......	0 Com.	Com. 4	0 8				
Mytilus edulis	......	12 292S	32 464S	20 8	4 28	16 8				
Mya arenaria	......	......	40S 8S	20S 0	12S 20S	....	4S 0			
Thais lapillus	......	......	0 100	0 64	28 32	0 8	4 8	12 36	8 0	
Lumbrinereis tenuis	......	......	50 28	....	0 40	....	4 0	20 0	0 12	
Gammarus locusta	......	......	....	0 4	12 40	....	....	8 Com.	8 8	
Neopanope sp.	......	......	....	....	0 1	....	0 1			
Ascophyllum nodosum	......	......	....	....	Abun. Abun.	Abun. Abun.	Abun. Abun.	Abun. Abun.	Abun. Abun.	
Sertularia pumila	......	......	....	....	....	Com. 0	0 Com.			
Carcinides maenas	......	......	....	....	....	....	0 1	1 1		
Spirorobis spirorbis	......	......	....	....	....	....	100 0	400 400	600 400	— 48
Asterias vulgaris	......	......	....	....	....	....	1 1	0 1	0 1	— 1
Schizoporella unicornis	......	......	....	....	....	....	12 sq. in. 5 sq. in.	16 sq. in. Abun.	— 4 sq.in.	
Gemellaria loricata	......	......	....	....	....	....	8 0	20 Com.	— 1	
Acmaea testudinalis	......	......	....	....	....	....	4 0	8 0	— 8	
Anomia simplex	......	......	....	....	....	....	....	0 2		
Strongylocentrotus drobachiensis	......	......	....	....	....	....	....	0 1		
Crepidula fornicata	......	......	....	....	....	....	....	0 4	— 4	
Chondrus crispus	......	......	....	....	....	....	....	......	Com.	
Lichenophora hispida	......	......	....	....	....	....	....	......	— 1 sq.in.	

TABLE 9. Station P. Rocky shore. Top number sample of 7-31-35, middle number sample of 7-31-36, and bottom number sample of 8-3-37. Legend as on Table 4.

	1 S.H.W.L.	2 6D;22L	3 6D;28L	4 6D;36L	5 6D;36L
Orchestia platensis........	0 12 4				
Terrestrial arthropods.....	84 56 52				
Littorina saxatilis........	....	0 124 12			
Isopod...................	....	0 0 8	4 0 0		
Mytilus edulis...........	....	0 28 0	16 2 0	24 4 0	40 0 0
Anurida maritima........	....	20 0 0	400 32 12	1200 20 0	0 0 12
Balanus balanoides.......	....	80 1600 108	2800 1200 1480	3000 0 1108	4800, 16 1400
Littorina littorea..........	....	28 104 4	84 0 16	40 0 48	180 160;2108 496
Littorina obtusata........	....	....	84 24 60	100 48 60	
Ascophyllum nodosum.....	....	....	Abun. Abun. Abun.	Abun. Abun. Abun.	
Sertularia pumila.........	....	....	0 Com. 0	Abun. Abun. Abun.	
Thais lapillus............	....	....	0 2 0	4 32 20	8 8 12
Gammarus locusta........	....	....	....	4 8 0	
Bryozoan.................	....	....	....	0 1 sq.in. 3 sq.in.	
Clava leptostyla..........	....	....	....	0 0 8	
Chondrus crispus.........	....	....	....	0 0 Sm.Amt.	
Cancer irroratus..........	....	....	....	....	0 0 1

Activity in this community when exposed is much the same as that of the Balanus-Mytilus Faciation. The snails *L. littorea* and *L. obtusata* continue to feed on algae, especially under the moist heaps of Ascophyllum; scavenging arthropods (Gammarus, Orchestia, Anurida) are active, but all under cover except Anurida. The strewn masses of brown seaweeds serve as a haven for the motile animals and the stranded subtidal animals for protection against predators and desiccation. Shallow tidal pools, when present, allow some of the intertidal organisms to continue their activities as though there were no tidal rhythm. The herring gull and crow comb the shores for food.

As the water covers the lowest zone, the bryozoans

(Lichenophora, Schizoporella, etc.), sedentary snails (Acmaea, Crepidula), Spirorbis, and Anomia resume their feedings. Strongylocentrotus (sea urchin), when present, continues its movements.

Upon reaching the mean-low-water line, the water

FIG. 9. Rocky shore at station B inhabited by the Balanus-Mytilus-Ascophyllum faciation. This type is found on the shores of Gloucester Harbor at the extremity of the inlet. Stakes indicate certain quadrat levels.

FIG. 10. Rocky shore at station P inhabited by the Balanus-Mytilus-Ascophyllum faciation. This type is found along exposed ledges bordering the inlet. Stakes indicate quadrat levels.

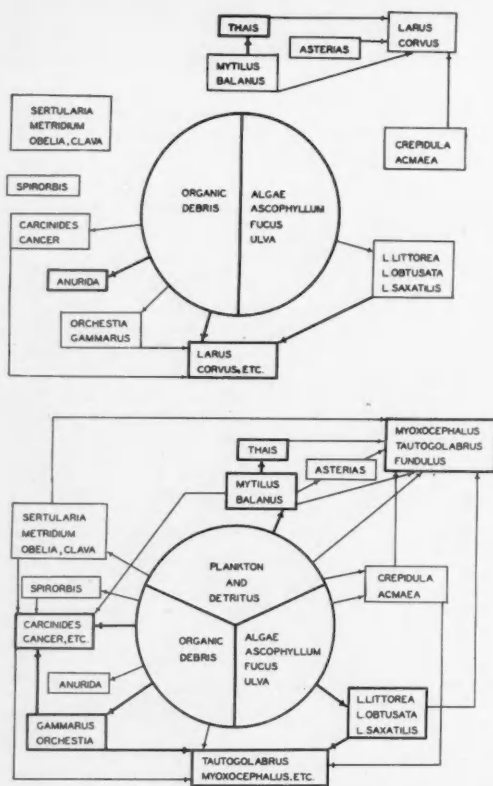Fig. 11. The Balanus-Mytilus-Ascophyllum faciation on glacial boulders at station T. Stakes indicate quadrat levels.

Fig. 12. Food coactions of the Balanus-Mytilus-Littorina biome.

begins to float the brown algae (Ascophyllum, Fucus) which remain attached to the rocks at one end and float freely at the other. On the seaweeds, Sertularia and Clava once again have access to the plankton, and *L. littorea* and *L. obtusata* crawl about, scraping away the plant tissue. Mytilus and Balanus resume feeding from this point back to the upper limit of

their distribution, and Thais and Asterias continue their predation on them.

Gammarus and other amphipods often take to swimming when submerged while the insects (Tabanus, Culicoides, etc.) leave the shore.

Crabs (Carcinides, Cancer, Pagurus) and fishes (sculpins, minnows, cunner) come upon the shore to feed on the wealth of the invertebrates present. About middle shore and higher, Neopanope and Tanais, which hide under loose stones during low tide, become active again; likewise for *Littorina saxatilis* on the rock surfaces where they remain dormant until submerged.

Anurida is driven into air bubbles under loose stones and among gravel or else onto higher ground. Above mean-high-water line the seaweeds and their associated animals are not present. *L. saxatilis*, Orchestia, and terrestrial arthropods compose the community at this level. Orchestia is driven into the seawrack, and at flood tide the terrestrial spiders, isopods, mites, and insects are driven out to the water line or floated upon the flood waters. Terns and kingfishers take the place of gulls and crows as the community becomes inundated.

Annuation and Succession

Mytilus edulis was very abundant everywhere in 1933 and was increasing and spreading the following season. In 1935, however, this mussel was removed from certain flats to prevent its encroachment upon the clam flats. In 1936 abundant seed mussels invaded the uncovered sediments; but in 1937 the Bureau of Marine Fisheries removed thousands of bushels of blue mussels in its campaign to restore the soft-shell clam. By 1940, this prolific mussel was successfully invading many of the areas which had been cleared.

Littorina saxatilis underwent a most remarkable fluctuation in abundance during the period of this study. In 1933 no living specimen was found although the presence of numerous shells indicated that it had been abundant in recent years. In 1934, less than a dozen living snails of this species could be found. The following summer, however, this snail was exceedingly abundant on all shores of the inlet, and in many cases was found out of its normal vertical range and habitat. Mud, rocks, seaweeds, and marshes were peppered with it. In 1936 it was still more abundant at certain levels, but was restricted more to the higher tidal levels and for the most part confined to solid surfaces—rocks, blades of thatch grass, and the firm marsh banks. An average of two snails per square inch was found over a wide area. By the next summer the population density had dropped to about the 1935 level and this snail remained on the higher shore levels.

Littorina obtusata, the seaweed snail, was more common in 1934 than during the previous year, in many places being as abundant as the introduced periwinkle, *L. littorea*. In 1935 it was often more abundant than *L. littorea* on some shores. During the following two years, *L. obtusata* gradually de-

cline in numbers. *L. littorea* withstood the low temperatures (−20° F.) of the winter of 1933-34 very well, large populations being found in December and March, with an unusually large number of young snails found in March, but the following year this species declined somewhat in abundance, and on many shores was overshadowed by the expanding populations of *L. saxatilis* and *L. obtusata*. In 1936 it returned to its usual abundance. Orton & Lewis (1931) reported on changes in snail populations after a severe winter in an English estuary. *L. littorea*, introduced from the British Isles, was first observed in this section of North America in Salem Harbor in 1872, and by 1880 was one of the most abundant snails along the Massachusetts coast (Morse 1880).

In years preceding this survey, the writer had observed *Thais lapillus*, the rock snail, on many rocky shores of the inlet. In 1933, however, very few specimens could be collected, and those that were found were taken at the extremities of the inlet bordering Gloucester Harbor and Ipswich Bay. Empty shells along the inlet reminded one of its former range and abundance. In 1934 it began to return, increased to a noticeable degree the following year when many young snails were observed and at that time as many as 24 could be collected in a 400-square-inch quadrat. The next year collections quadrupled. In 1937 the species was once again an abundant member of the hard surface communities, and by 1940 it was as common as ever observed in the inlet.

Acmaea testudinalis was collected in greater quantity in 1934 than during other years. A crab of the genus Neopanope, found in abundance under rocks in 1933, disappeared from the collections in 1934, possibly because of the low temperatures of the intervening winter. It returned in 1935 in small numbers and gradually increased in abundance each year. *Metridium dianthus* suffered a severe set back in the season of 1936 because of fresh coats of tar which were applied to the pilings of the railroad trestle. These pilings had been one of the principal habitats of this sea anemone. Shelford et al. (1935) described changes in barnacle populations between 1928 and 1930 on the Pacific coast and called attention to the importance of annuation in the study of marine communities. Rice (1930) and Towler (1930) made studies on these same barnacle communities.

With the continuation of sedimentation, silt and sand cover the lower margins of the rocky shores. Pockets of sediment among the rocks lead to the establishment of the bivalve-annelid biome as isolated outposts within the hard-surface community. The mussel beds can keep up with the accumulating sediments by constructing layer upon layer of new sets of mussels. Eventually, however, when the elevation reaches the level of the thatch grass marshes, *Spartina glabra* invades the mussel beds and the pockets of sediments among the rocks as well as the higher levels of sand beaches and mud flats (Figs. 5, 8, 13). In time, the low marsh community S. glabra-L. saxatilis-Brachidontes Associes becomes established.

COMMUNITIES OF SUCCESSION TO LAND

Bordering the Mya-Nereis pelagica and Balanus-Mytilus-Littorina Biomes are two marsh communities which are transitional between them and land communities. These are designated as the Spartina glabra-Littorina saxatilis-Brachidontes Associes and the Spartina patens-Melampus-Orchestia Associes. It is well known that marshes are extensively developed along shores that are gradually subsiding (Ganong 1903, McAtee 1935). The entire inlet at Cape Ann is bordered by the two marsh communities mentioned, commonly referred to as the low marsh (mid-littoral marsh of Johnson & York 1915) and the high marsh. Observations show that these marsh communities develop on all kinds of bottom materials. Along the inlet they are found on sand, mud, old mussel beds, and among rocks. Ganong (1903) made an extensive study of the Bay of Fundy marshes and mapped out their distribution. Johnson & York (1915) correlated marsh types and vegetation zones with tidal levels at Cold Spring Harbor. Johnson & Skutch (1928, pt. III) described marsh zones and traced marsh succession to a spruce climax on Mt. Dessert Island. Prat (1933) discussed the relation of marsh lands to mud flats and sand beaches. McAtee (1935) outlined the general features of the marshes on the east coast of North America with an annotated list of the vertebrate fauna. Chapman (1938-1940), in a series of studies on salt marshes in the British Isles and the eastern coast of North America, described them and their algal communities in detail. A thorough analysis was made of the tides, water table, drainage, aeration, and salinity, and comparisons made between British marshes, and between those at Long Island, N. Y., Lynn, Mass., and the Scott marshes of England. In another paper (Chapman 1940a) he outlined the successions of east coast North American marshes.

SPARTINA GLABRA-LITTORINA SAXATILIS-BRACHIDONTES ASSOCIES

General Character

The Spartina glabra-Littorina saxatilis-Brachidontes Associes occupies the marsh banks between the lower shores and the high marshlands. These banks are for the most part steep and narrow and have a vertical height of about five feet, ranging up to the mean-high-water line. Johnson & York (1915) found this marsh at Cold Spring Harbor between 1.5 and 6.5 above mean-low-water line. With the exception of breaks caused by the rocky shores and ledges, the low marshes at Cape Ann form a continuous line along either side of the channel from end to end. This associes was studied at Stations F, I, J, L, N, O, and Q, (Tables 6, 10; Figs. 13-17). Thirty-six quadrat counts were made.

Dominants and Slow-Moving Influents

Dominants

Spartina glabra, thatch grass, Abun./100
Littorina littorea, periwinkle, 80/97
L. saxatilis, snail, 75/84
Ascophyllum nodosum f. scorpioides, marsh seaweed, Com./40

TABLE 10. Station J. High marsh, low marsh, and edge of mud flat. Top number sample of 8-24-35; bottom number sample of 8-26-36. Legend as on Table 4.

	1 Near S.H.W.L.	2 21D;4L.	3 21D;1.5L.	4 26D;1.5L.	5 40D;4.5L.	6 14D;52L.	7 21D;25L.	8 21D;7L.
Spartina patens	Abun. Com.	Abun. Abun.	Abun. Abun.	Abun. Abun.				
Isopod	20 12	8 4	....	4 0				
Orchestia platensis	16 24	20 12	28 12	0 16	10 4	1 0		
Melampus bidentatus		48 16	116 36	72 56	0 32			
Talorchestia longicornis	....	8 0	....	....	1 0			
Littorina saxatilis	....	....	....	8 0	400 124	50 24		
Littorina obtusata	....	....	....	....	1 0			
Spartina glabra	....	....	....	....	Com. Com.	Com. Com.		
Anurida maritima	....	....	....	....	10 0	7 20		
Littorina littorea	....	....	....	....	35 52	300 48		
Mytilus edulis	....	....	....	....	....	48 128		
Brachidontes demissus	....	....	....	....	....	17 1;258		
Nassarius obsoletus	....	....	....	....	....	3 0	25 28	— 56
Cyathura carinata	....	....	....	....	....	....	1 1	
Nereis pelagica	....	....	....	....	....	....	4 0	— 4
Mya arenaria	....	....	....	....	....	....	2 4	— 8
Lumbrinereis tenuis	....	....	....	....	....	....	4 0	--- 4
Macoma balthica	....	....	....	....	....	....	1 0	--- 8

Subdominant
Brachidontes demissus, ribbed mussel, 8/25
　Influents
Gammarus locusta, amphipod, 109/33
Anurida maritima, insect, 68/77
Littorina obtusata, seaweed snail, 37/37
Fucus vesiculosis, brown alga, Com./20
Coelopa frigida, kelp fly
Culicoides sp., midge
Tabanus nigrovittatus, horse fly
Aedes sollicitans, salt marsh mosquito
Fucellia sp., kelp fly
　Subinfluents
Mytilus edulis (seed), blue mussel, 29/57

Orchestia platensis, amphipod, 10/27
Balanus balanoides, barnacle, 94/30
Fucus vesiculosis v. spiralis, brown alga, Num./10
　　　　Permeant Influents
Carcinides maenas, green crab
Cancer irroratus, rock crab
Fundulus heteroclitus, minnow
Butorides virescens, green heron
Nycticorax nycticorax, night heron
Corvus brachyrhynchos, crow
Charadrius semipalmatus, semipalmated plover
Actitis macularia, spotted sandpiper
Pisobia minutilla, least sandpiper
Tyrannus tyrannus, kingbird

Iridoprocne bicolor, tree swallow
Hirundo erythrogaster, barn swallow
Dumetella carolinensis, catbird
Sturnus vulgaris, starling
Sturnella magna, meadowlark
Agelaius phoeniceus, red-wing
Quiscalus quiscula, bronzed grackle
Ammospiza caudacuta, sharp-tailed sparrow

Melospiza melodia, song sparrow
Secondary Forms
Melampus bidentatus, marsh snail
Anas rubripes, black duck

Organization and Coactions

This low marsh is dominated by a tall, solid stand (4-5 feet high) of thatch grass *(Spartina glabra)*. *L. saxatilis* is common on the stems and lower leaves of Spartina, usually attached by mucus during exposure. Intermingled at the base of the stems is a mass of *Fucus vesiculosus*, including *var. spiralis*, or *Ascophyllum nodosum f. scorpioides* or both. Abundant on these algae are *Littorina littorea* and *L. obtusata*, while *Gammarus locusta* remains under them or in tunnels in the bank. Crawling everywhere over the ground and algae is *Anurida maritima*, while Tabanus, Culicoides, and other dipterous insects are found throughout the marsh.

Brachidontes demissus (ribbed mussel) occupies the ground, being half embedded in the bank and half exposed, with the center of its population on the lower bank level. A number of blue mussels (Mytilus) usually become attached here to some convenient anchorage, and *Balanus balanoides* seed is often

FIG. 13. Low marsh community, Spartina glabra-Littorina saxatilis-Brachidontes associes, invading upper level of mud flat at station J. Notice Nassarius obsoletus scattered over surface of mud.

FIG. 15. Junction of the low marsh and high marsh communities at mean-high-water line at station J.
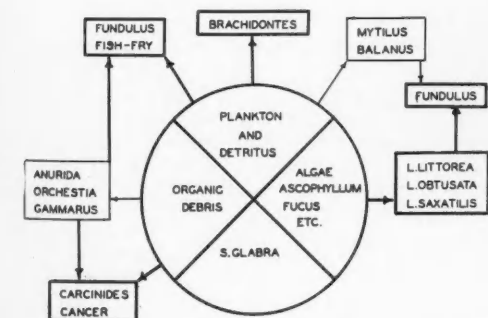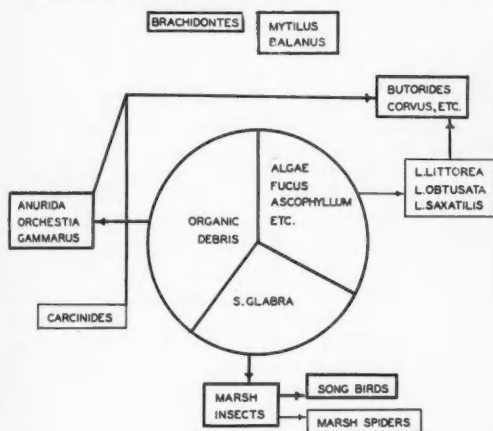
FIG. 14. Food coactions of the Spartina glabra-Littorina saxatilis-Brachidontes associes of low marshes.

FIG. 16. Tidal creek at station F with marsh banks of low marsh Spartina glabra-Littorina saxatilis-Brachidontes associes and with high marsh plateau of S. patens-Melampus-Orchestia associes.
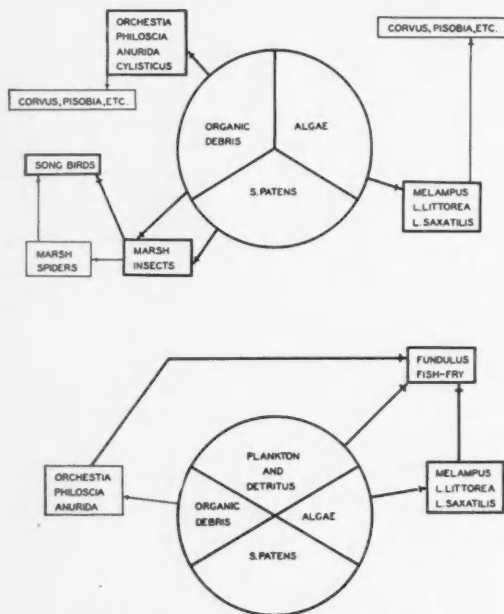
FIG. 17. Food coactions of the Spartina patens-
Melampus-Orchestia associes of high marshes.

abundant, adhering to the mussels, to small rocks,
old plant stems, and occasionally to algae or the
marsh bank itself. *Nassarius obsoletus* on the muddy
sediments often penetrates the lower edge of this
marsh community. On the higher level small num-
bers of mites, spiders, and insects are present while
on the top ridge, Orchestia, Philoscia (crustaceans),
and Melampus (marsh snail) overlap from the high
marsh community.

During exposure snails of the genus Littorina are
generally quiescent, as elsewhere at time of low-water,
although a small number of the seaweed snail (*L.
obtusata*) may be active. Anurida, and to a less ex-
tent some of the amphipods, are feeding at this time.

The typical marsh insects (Tabanus, Culicoides,
Aedes, etc.) are feeding on debris and marsh plants,
while they are fed on by the marsh spiders, both
groups falling prey to the passerine birds (kingbird,
swallows, meadowlark, redwing blackbird, sparrows,
etc.) which visit here. Shore birds and herons pick
up various invertebrates among the thatch grass.

About one foot below half-tide level, the water
begins to contact the low marsh community. The
scattered mussels and barnacles begin to take in
plankton and detritus again after several hours of
inactivity. As the water continues to rise the three
Littorina snails become more active and feed on the
algae. Gammarus is able to swim about and Brachi-
dontes opens its shells and extends its siphons.
Anurida is driven back up the shore or into air
pockets in the marsh. The marsh spiders and in-
sects also retreat. *L. saxatilis* migrates up the shore

to a certain extent, especially during the days of
spring tides when the shore is flooded to a maximum
and the marsh is covered to a greater depth than
usual. The common crabs (Carcinides, Cancer),
minnows (Fundulus), and fish fry invade the low
marsh zone and feed on debris and various inverte-
brate animals.

Annuation and Succession

On some shorelines the low marsh retreated each
year because of wave action which cut into the marsh
banks, undermined the growth of *Spartina glabra*,
and caused fragments of the marsh banks to break
away. Another contributing cause was the action of
ice in winter time which broke down the edges of
the marsh banks and pushed fragments of the thatch
grass community and its sod out onto the mud flats
(see right hand corner of Figure 6.). On the other
hand, where wave action was not severe, the banks
were not undermined and consequently there was no
abrupt edge which could be torn down by ice action.
In these protected marshes the junction between them
and mud flats, beaches, mussel beds, or rocky shores
was sharply defined but on a gradual slope. As sedi-
mentation continues, the low marsh community in-
vades these other communities of the tidal zone (Fig.
13) as discussed earlier.

The sudden and pronounced increase of *Littorina
saxatilis* is discussed in the section on annuation of
hard-surface communities, and the drastic decline and
eventual return of *Carcinides maenas* are accounted
for in the discussion of the subtidal community.
Brachidontes demissus was collected in greater abun-
dance in 1936 than in other years. This was a suc-
cessful year for the seeding-in of this ribbed mussel,
which accounted for the greater density that year.

As the S. glabra-L. saxatilis-Brachidontes Associes
is slowly elevated to the mean-high-water line, it is
replaced by the high marsh community, the Spartina
patens-Melampus-Orchestia Associes. The junction
between the two is usually abrupt and follows the
mean-high-water contour (Fig. 15, 16). Above this
level, broad and extensive marshes of the fox grass
(*Spartina patens*) predominate to the spring-high-
water line.

SPARTINA PATENS-MELAMPUS-ORCHESTIA ASSOCIES
General Character

The high marsh is a very gently sloping, almost
level expanse of soggy, peaty ground built up by
deposition and peat formation between mean-high-
water line, where the low marsh ends, and spring-
high-water line. It is populated by an almost solid
stand of *Spartina patens*. Johnson & York (1915)
believed that this species is held at this level by com-
petition with *S. glabra* that occupies the next lower
zone, and they found *S. patens* at lower levels in the
absence of *S. glabra*. Along the Annisquam River,
however, the two are nearly always found adjacent at
their respective levels, even on newly developing
marshes. Both species, according to Chapman (1940),
reproduce chiefly by rhizomes. He found very few

viable seeds on the marshes at Lynn. Wherever *S. patens* has been removed for one reason or another, there is a patch of *Salicornia europaea*. This plant is slowly replaced by the fox grass.

Dominants and Slow-Moving Influents
Dominants
Spartina patens, fox grass, Abun./100
Orchestia platensis, beach flea, 23/90
Melampus bidentatus, marsh snail, 47/50
  Subdominants
Littorina littorea, periwinkle, 53/40
Philoscia vittata, isopod, 7/50
  Influents
Littorina saxatilis, snail, 5/40
Terrestrial arthropods (insects, sowbugs, spiders, mites)
Anurida maritima, insect, 20/10
Culicoides sp., midge
Tabanus nigrovittatus, horsefly
Aedes sollicitans, salt marsh mosquito
  Subinfluents
Salicornia europaea, saltwort
Limonium carolinianum, marsh rosemary
Permeant Influents
Pisobia minutilla, least sandpiper
Charadrius semipalmatus, semipalmated plover
Corvus brachyrhynchos, crow
Buteo lineatus, red-shouldered hawk
Circus hudsonius, marsh hawk
Actitis macularia, spotted sandpiper
Tyrannus tyrannus, kingbird
Iridoprocne bicolor, tree swallow
Hirundo erythrogaster, barn swallow
Dumetella carolinensis, catbird
Sturnus vulgaris, starling
Sturnella magna, meadowlark
Agelaius phoeniceus, red-wing
Quiscalus quiscula, bronzed grackle
Ammospiza caudacuta, sharp-tailed sparrow
Melospiza melodia, song sparrow
Microtus pennsylvanicus, field mouse
Sylvilagus transitionalis, cottontail
Thamnophis sirtalis, garter snake
Fundulus heteroclitus, minnow
Secondary Forms
Distichlis spicata, spike grass
Puccinellia maritima, sea spear
Juncus gerardi, black grass
Gerardia maritima, seaside gerardia
Plantago decipiens, seaside plantain
Solidago sempervirens, seaside goldenrod
Anas rubripes, black duck

Organization and Coactions

In these marshes shore and song birds are common everywhere flying over the marsh and walking among the grass. Among the matted stems of Spartina are the snails, Melampus, *Littorina littorea*, and *L. saxatilis*, a beach flea (Orchestia), an isopod (Philoscia), and marsh spiders, mites, and insects. These species are scattered about more or less evenly throughout. Either among the grass or in the air will be found the horsefly (Tabanus), midge (Culicoides), black fly (Coelops) and similar insects which inhabit these marsh communities.

Along spring-high-water line there is an ecotone or transition belt between the fox grass marsh com-munity proper and the terrestrial communities. Near the upper limit of *S. patens*, the marsh rosemary *(Limonium carolinianum)* and seaside goldenrod *(Solidago sempervirens)* dominate, while along the highest ridge black grass *(Juncus gerardi)* and its associates *(Distichlis spicata, Puccinellia maritima, Plantago decipens, Gerardia maritima)* dominate. The animal population of this ecotone consists chiefly of terrestrial insects, spiders, mites, isopods, snails, song birds, and small mammals.

Even during the long exposure Melampus, Orchestia, and Philoscia are found scattered about rather generally under the fox grass or marsh hay *(S. patens)* and are quite active. *L. littorea* and *L. saxatilis* are more dormant. Marsh and terrestrial insects are abundant, flying in the air or living among the grass where they fall prey to spiders. The song birds feed on them while shore birds search the high marshes for snails and crustaceans. Davenport (1903) has shown the typical chain on the high marshes at Cold Spring Harbor to be: "debris feed-ers → predaceous spiders, robber flies, tiger beetles → swallows."

Each fortnight as the spring tides (equinoctial tides) spread over the high marsh communities, the spiders and insects are floated or driven off. Melam-pus and *L. saxatilis* are driven back to a higher level or climb to the top of the grass, and the birds go elsewhere for a time. As the seawrack along the highwater line is submerged, the isopods, spiders, and insects are driven out. Fundulus (minnow) and fish-fry swim over the flooded marsh and pick up the various small snails and crustaceans.

A number of crabs (Careinides), king crabs (Limulus) and shrimps (Crago) likewise invade the high marsh at this time, and the motile animals in general move to a higher level. After the retreat of the water, snails, especially of the genus Littorina, are found in large numbers along the highest margin of the shoreline with the center of the population of each some two feet above the normal distribution. The S. patens-Melampus-Orchestia Associes was studied at Stations F, I, J, L, O, Q, T, and U, in-cluding 28 quadrat counts (Tables 6, 10; Figs. 15-17).

Annuation and Succession

Spartina patens with its associated animals is slowly but definitely filling in the marsh creeks, coves, and the margins of the inlet. This process is pro-ceeding more slowly than the succession taking place in communities of lower levels since the high marshes are inundated only at times of spring tides. During the interval of this study no significant change could be observed.

One of the characteristic marsh snails, *Melampus bidentatus*, was observed to increase to a noticeable degree. In 1933 it was found locally in the marshes, but numerous shells in the seawrack along the entire shoreline indicated a greater abundance in past years. In 1935 it was more abundant and widely distributed. It had increased to as many as 115 in a 400 square inch quadrat.

CLIMAX. BEECH-MAPLE ASSOCIATION

The climax land community of Cape Ann is the Beech-Maple Association of the Temperate Deciduous Forest Biome. Some of the principal dominants are beech, sugar maple, red oak, black oak, white oak, elm, white pine, pitch pine, and hemlock. Cape Ann is within the Transition Zone, possessing both deciduous and coniferous trees, but with a decided majority of hard woods. The conifers may be regarded as forming a mictium with the deciduous trees, or they may be regarded as persistent relics from the last post glacial period.

Most of the original land vegetation bordering the inlet has been destroyed, but in places, climax or subclimax trees are still found. Much of the riparian zone contains a poor, gravelly soil, and probably had not developed a climax community before disturbance took place. Above station R there is a small area of climax beech woods with the characteristic red backed salamander *(Plethodon cinereus)* and at Ravenswood Park, a nearby preserve area, is found a tract of climax Beech-Maple-Hemlock forest.

SUMMARY AND CONCLUSIONS

An ecological study of the organization and dynamics of the marine communities of a tidal inlet (Annisquam River) at Cape Ann, Massachusetts, carried out principally during the summer seasons of 1933-1937 inclusive, has brought forth the following conclusions.

1. The marine communities are divisible into the following:
   a. Scomber-Calanus Biome of the pelagic realm. This community within the inlet is recognized as the Clupea-Syngnathus Faciation.
   b. Strongylocentrotus-Buccinum Biome of the subtidal bottom. The inlet portion of this community is designated as the Laminaria-Cancer Faciation.
   c. Mya-Nereis pelagica Biome occupies intertidal, loose bottom sediments.
      1. Talorchestia Faciation occupies coarse sediments.
      2. Macoma-Clymenella Faciation occupies fine sediments.
   d. Balanus-Mytilus-Littorina Biome occupies hard surfaces.
      1. Balanus-Mytilus Faciation, found primarily over sediments.
      2. Balanus-Littorina-Ascophyllum Faciation, found primarily on rocks.
   e. Communities of succession to land.
      1. Spartina glabra-Littorina saxatilis-Brachidontes Associes occupies the low marshes, particularly marsh banks.
      2. Spartina patens-Melampus-Orchestia Associes occupies the high marshes.

2. Narrow ecotones exist between the major communities resulting from an overlapping of characteristic species along the spring-tide levels. Ecotones were found between the following communities:

a. Laminaria-Cancer Faciation and Mya-Nereis pelagica Biome along the spring-low-water margin.
b. Laminaria-Cancer Faciation and Balanus-Mytilus-Littorina Biome along the spring-low-water margin.
c. Spartina patens-Melampus-Orchestia Associes and terrestrial communities along the spring-high-water margin.

3. An intermingling of communities results from a mixture of sediments and hard bottom materials, and developments in physiographic succession. Fragments of the Balanus-Mytilus-Littorina Biome are found scattered in the Mya-Nereis pelagica Biome and vice versa, giving rise to a condition comparable to the terrestrial savanna or parkland community.

4. The precise zonation of intertidal communities and their components (which has been demonstrated by many investigators), is the only method by which these communities can be studied. Quadrat sampling is of significance in the study of tidal communities only in so far as the level of examination is known, with consequent relationship to exposure and submergence.

5. There is a rhythmical change in the composition and dynamics of the communities associated directly with the tidal flow and ebb. The organization and coactions of intertidal communities are markedly different at low-tide and at high-tide, the transformation taking place gradually and uniformly during fluctuation of the tide. Terrestrial and marsh animals feed on the intertidal zone when it is exposed. They invade the shore during ebb tide following down the water line as it retreats, and are forced back from the feeding grounds gradually as the tide returns. Subtidal permeant animals feed on the intertidal zone when it is submerged. They advance upon the shore with the incoming tide, some species being immediately behind the front wave of water. Intertidal animals for the most part remain inactive during exposure, resuming locomotion and feeding when submerged.

6. Each year significant differences were found in the major communities as a result of the fluctuation of abundance of certain species. Some of the most striking and important changes observed involved the following species: *Zostera marina, Lacuna vincta, Polinices heros, Carcinides maenas, Asterias vulgaris, Mya arenaria, Nereis pelagica, Nassarius obsoletus, Mytilus edulis, Littorina saxatilis, L. obtusata, Thais lapillus,* and *Melampus bidentatus.*

7. While the marine communities inhabiting the Annisquam inlet are similar to climax communities found elsewhere, within the inlet they are undergoing successional changes as the result of sedimentation which is gradually filling the inlet and which has several times in the past nearly obliterated it as an open inlet from the ocean. Periodic dredging is necessary to maintain the waterway. The Mya-Nereis pelagica Biome of marine sediments is extended as the bars and flats are enlarged

TABLE 11. Systematic Arrangement and Ecological Evaluation of the Common Macroscopic Organisms of the Marine Communities at Cape Ann, Massachusetts.

1. Clupea-Syngnathus Faciation of the Scomber-Calanus pelagic biome. * indicates presence in Ipswich Bay but not in the Annisquam River.
2. Strongylocentrotus-Buccinum Biome of the Ipswich Bay bottom.
3. Laminaria-Cancer Faciation of the Annisquam River bottom.
4. Mya-Nereis pelagica Biome of tidal sediments.
5. Balanus-Mytilus-Littorina Biome of tidal hard surfaces.
6. Spartina glabra-Littorina saxatilis-Brachidontes Associes of the low marshes.
7. Spartina patens-Melampus-Orchestia Associes of the high marshes.

D=Dominants　　　　PI=Permeant influents
SD=Subdominants　　SF=Secondary forms
IF=Influents　　　　IC=Incidentals
SI=Subinfluents

	1	2	3	4	5	6	7
ALGAE							
Chlorophyceae							
Enteromorpha intestinalis (L.)		SI	SF				
Ulva lactuca L.		D	D	SI	IC	IC	
Chaetomorpha linum (Muller)		SF	SD	IF			
Chaetomorpha spp.		SI				SF	
Cladophora rupestris (L.)							
Phaeophyceae							
Chordaria flagelliformis (Muller)		SI					
Chorda filum (L.)		SI	SF				
Agarum cribrosum (Mert.)		D					
Laminaria longicruris De la Pylaie		D	D				
Laminaria saccharina (L.)		D	D				
Laminaria digitata (L.)		SD	IC		SF		
Fucus edentatus De la Pylaie					SD	IF	
Fucus vesiculosus L.						SI	
Fucus vesiculosus V. spiralis							
Ascophyllum nodosum (L.)					D		
A. nodosum f. scorpioides (Hornemann)						D	
Ectocarpus sp.		SF	SF				
Rhodophyceae							
Porphyra umbilicalis (L.)		SI	SF				
Euthora cristata (L.)		D	IF				
Chondrus crispus (L.)		D	IF				
Gigartina stellata (Stackhouse)		SI	IC				
Rhodymenia palmata (L.)		SI	SF				
Plumaria pectinata (Gunner)		SF	IC				
Ceramium rubrum (Hudson)		SF	IC				
Polysiphonia lanosa (L.)					SF		
Lomentaria baileyana (Harv.)		SI	SF				
Callithamnion sp.		SD	SF				
Corallina officinalis L.		SI					
Angiospermae							
Zostera marina L.		IC	IC				
Spartina glabra Muhl.					D		D
Spartina patens (Ait.)							SF
Distichlis spicata (L.)							SF
Puccinellia maritima (Huds.)							SF
Juncus gerardi Loisel							SI
Salicornia europaea L.							
Limonium carolinianum (Walt.)							SI
Gerardia maritima Raf.							SF
Plantago decipiens Barneoud							SF
Solidago sempervirens L.							SF
Porifera							
Leucosolenia sp.		IC					
Sycon ciliatum (Fahr.)		IC					
Suberites compacta Verrill		SF	IC				
Chalina oculata (Pallas)		SF	SI				
Chalina arbuscula Verrill		SF	SI				
Coelenterata							
Clava leptostyla Agassiz					SF		
Hydractinia echinata (Fleming)		IC	SF				
Corymorpha pendula Ag.		SF					
Tubularia spectabilis (Ag.)		SF	SF		SF		
Sertularia pumila L.		SI	SI		SF		
Abietinaria abietina (L.)		SF	SI				
Campanularia flexuosa (Hincks)							
Obelia spp.		SF	SF		SF		
Cyanea capillata (L.)	IF						
Aurelia aurita (L.)	IF						
Metridium dianthus (Ellis)		SF	SF		SF		
Platyhelminthes							
Bdelloura propinqua (Wheeler)			IC				
Leptoplana variabilis (Girard)		SF	SF				
Cerebratulus lacteus (Leidy)		SF	SF	SI			
Bryozoa							
Lichenophora hispida Fleming		IC	SF				
Gemellaria loricata (L.)			SF		SF		
Electra pilosa (L.)		SF	SF				
Cellaria fistulosa (L.)		SF	SF				
Bugula turrita (Desor)		SI	SI				
Bugula flabellata (Thompson)		SI					
Schizoporella unicornis (Johnston)		IC	IC		SF		
Flustrella hispida (Fabricius)			SF		IC		
Membranipora sp.		SF	SF				
Annelida							
Lepidonotus squamatus (L.)		IF	IF				

TABLE 11. (Continued)

	1	2	3	4	5	6	7
Lepidonotus sublevis Verrill		IF	IF				
Phyllodoce catenula Verrill				IC			
Nereis pelagica I		SF	SF	D			
Lumbrinereis tenuis (Verrill)		IF	IF	D			
Glycera dibranchiata Ehlers				IF			
Enoplobranchus sanguineus Verrill				SF			
Clymenella torquata (Leidy)			SF	D			
Spirorbis spirorbis (L.)		IF	SF		SI		
Hydroides sp.		SI					
ARTHROPODA							
Crustacea							
Balanus balanoides (L.)				SF	D	SI	
Balanus eburneus Gould		IC	SF				
Balanus crenatus Bruguiere		IC	SF				
Hyperia galba (Montague)	IC						
Orchestia platensis Kryer					SI	SI	D
Talorchestia longicornis (Say)				IF			
Allorchestes sp.				IF			
Gammarus locusta (L.)		IF	IF	IF	IF	IF	
Carinogammarus sp.		IF					
Caprella acutifrons Latreille		IF	IF	SF			
Aeginia longicornis Kryer		IF	SF				
Amphipoda (unidentified)		SI	SI				
Cyathura carinata (Kryer)				SF			
Idothea baltica (Pallas)		IF	SF	SF			
Philoscia vittata Say							SD
Isopoda (unidentified)		IF	SI				
Crago septemspinosus (Say)		PI	PI	PI			
Palaemonetes vulgaris (Say)		PI					
Homarus americanus Milne-Edw.		PI	PI				
Pagurus longicarpus Say		PI	PI	PI	PI		
Pagurus pollicaris Say		PI	PI	PI	PI		
Libinia emarginata Leach		PI					
Cancer irroratus Say		PI	PI	PI	PI	PI	
Cancer borealis Stimpson		PI	SF	IC			
Neopanope sp.			SI		SI		
Carcinides maenas (L.)		SF	PI	PI	PI	PI	
Arachnoidea							
Limulus polyphemus L.			PI	PI			
Insecta							
Anurida maritima Lab.				SI	SI	IF	IF
Coelopa frigida Hald.					SI	IF	
Culicoides sp.						IF	IF
Tabanus nigrovittatus Macq.						IF	IF
Aedes sollicitans (Walker)						IF	IF
Fucellia sp.					SI	IF	
MOLLUSCA							
Amphineura							
Neomenia sp.		SI					
Chaetopleura apiculata (Say)		SF					
Gastropoda							
Onchidoris bilamellata (L.)			SF				
Aeolis sp.			SF				
Melampus bidentatus Say						SF	D
Acmaea testudinalis (L.)		IC	IC		SF		
Polinices heros (Say)		SD	D	SD			
Crepidula fornicata (L.)		SI	SI		SF		
Crepidula plana Say		SF	SF	SF			
Littorina littorea (L.)		IC	IF	SI	D	D	SD
Littorina saxatilis Olivi				SF	IF	D	SF
Littorina obtusata L.					IF	IF	
Lacuna vincta (Montague)		IF	SI				
Onoba aculeus Gould				SI			
Thais lapillus (L.)					IF		
Nassarius trivittata Say		SF	IF				
Nassarius obsoletus Say				IF			
Buccinum undatum L.		D					
Neptunea decemcostata (Say)		SD					
Colus stimpsoni Morch		SD					
Pelecypoda							
Solemya velum Say				SI			
Anomia aculeata L.		IC	IC		IC		
Anomia simplex D'Orbigny		SF	SF				
Mytilus edulis L.		IC	IF	SF	D	SI	
Modiolus modiolus (L.)		IF					
Arctica islandica L.		IF					
Brachidontes demissus Lam.						SD	
Cerastoderma pinnulatum Conrad			SF				
Mulinia lateralis Say				SF			
Gemma gemma (Totten)			SI	SI			
Petricola pholadiformis (Lam.)				IC			
Tellina tenera Say			SF				
Macoma balthica (L.)				SD			
Ensis directus Conrad				SI			
Siliqua costata (Say)		IF	SF	SF			
Mya arenaria L.			SF	D	IC		
Saxicava arctica		SF	SF				
Lyonsia hyalina (Conrad)			IC	IC			
Cephalopoda							
Loligo pealei Lesueur	IF						
Echinodermata							
Henricia sanguinolenta (O. F. Muller)		IF					
Asterias vulgaris Verrill		D	D	SF	IF		
Ophiopholis aculeata (L.)		SF	SF				

TABLE 11. *(Continued)*

	1	2	3	4	5	6	7
Strongylocentrotus drobachiensis (O. F. Muller)		D	D				
Echinarachnius parma (Lamarck)		D	SF				
CHORDATA							
Protochordata							
Dolichoglossus kowalevski (A. Ag.)				SF			
Botryllus schlosseri (Pallas)		SF	SF				
Cynthia carnea Verrill		SF					
Molgula manhattensis (DeKay)		SF	SF				
Boltenia ovifera (L.)		SF					
VERTEBRATA							
Pisces							
Caracharias taurus Raf	PI*	SD					
Isurus punctatus Storer	SD*	PI					
Raja erinacea Mitchill		D	SD				
Raja diaphanes Mitchill		SD	SD				
Anguilla bostoniensis (LeSueur)			PI				
Clupea harengus L.	D						
Salmo salar L.	SD*						
Pomolobus pseudoharengus (Wilson)	PI						
Osmerus mordax Mitchill	SD	PI	PI				
Fundulus heteroclitus (L.)		PI	PI	PI	PI	PI	PI
Syngnathus peckianus Storer	D	SF	SI				
Ammodytes americanus DeKay		PI					
Scomber scombrus L.	D						
Thunnus thynnus L.	SD*						
Pomatomus saltatrix (L.)	PI						
Poronotus triacanthus Peck	D	PI	PI				
Tautogolabrus adspersus Walbaum	PI	PI	PI	PI	PI		
Tautoga onitis L.	PI*	PI					
Myozocephalus scorpius (L.)		SD	D	PI			
M. aeneus Mitchill		SD	D	PI			
M. octodecemspinosus Mitchill		D	D	PI			
Pholis gunnellus L.		PI	PI				
Pollachius virens L.	D						
Merluccius bilinearis (Mitchill)	PI	PI					
Gadus morhua L.	SD	SD					
Melanogrammus aeglifinus L.		PI					
Urophycis tenuis (Mitchill)		SD	SD				
Urophycis chuss Walbaum		D	D				
Hippoglossus hippoglossus L.		PI					
Paralichthys dentatus L.		SD					
Pseudopleuronectes americanus Walbaum		D	D	PI			
Lophosetta aquosa (Mitchill)			SD				
Reptilia							
Chelonia mydas (L.)		PI	IC				
Thamnophis sirtalis (L.)							PI
Aves							
Phalacrocorax auritus auritus (Lesson)	PI						
Butorides virescens virescens (L.)				PI		PI	
Nycticorax nycticorax hoacti (Gmelin)				PI		PI	
Anas rubripes tristis Brewster				SF		SF	SF
Buteo lineatus lineatus (Gmelin)							PI
Circus hudsonius (L.)							PI
Charadrius semipalmatus Bonaparte				PI		PI	PI
Actitis macularia (L.)				PI		PI	PI
Pisobia minutilla (Vieillot)				PI		PI	PI
Larus argentatus smithsonianus Coues				PI	PI		
Sterna hirundo hirundo L.	PI						
Megaceryle alcyon alcyon (L.)	PI						
Tyrannus tyrannus (L.)						PI	PI
Iridoprocne bicolor (Vieillot)						PI	PI
Hirundo erythrogaster Boddaert						PI	PI
Corvus brachyrhynchos brachyrhynchos Brehm				PI	PI	PI	PI
Dumetella carolinensis (L.)							PI
Sturnus vulgaris vulgaris L.							PI
Sturnella magna magna (L.)							PI
Agelaius phoeniceus phoeniceus (L.)						PI	PI
Quiscalus quiscula aeneus Ridgway						PI	PI
Ammospiza caudacuta caudacuta (Gmelin)						PI	PI
Melospiza melodia melodia (Wilson)						PI	PI
Mammalia							
Microtus pennsylvanicus (Ord.)							PI
Sylvilagus transitionalis (Bangs)							PI
Phoca vitulina L.	SD						
Balaenoptera physalus (L.)	SD*						

and encrouch upon the Laminaria-Cancer Faciation of the subtidal bottom. These bars and flats in time become covered over by the Balanus-Mytilus Faciation. With the elevation of both this mussel bed community and the communities of the uncovered sediments up to a height of 4 feet within the mean-high-tide level, they are captured by the low marsh Spartina glabra-Littorina saxatilis-Brachidontes Associes. Accumulation of sediments among the rocks of the Balanus-Mytilus-Ascophyllum Faciation also leads to its replacement by the low marsh community. As this community is elevated to the mean-high-water line it is succeeded by the Spartina patens-Melampus-Orchestia Associes of the high marshes. At spring-high-water line the marine communities pass through a narrow ecotone to an upland terrestrial climax, the Beech-Maple Association of the Temperate Deciduous Forest Biome. Table 11 summarizes the ecological evaluation of the predominant species which compose these marine communities.

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SYMPOSIUM ON MARINE ECOLOGY

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INTRODUCTION

ALFRED C. REDFIELD

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A symposium on marine ecology was held on December 28, 1946, under the joint auspices of the Ecological Society of America and the Limnological Society on the occasion of the meeting of the American Association for the Advancement of Science in Boston.

It seemed appropriate to present to the many scientists coming from the interior of the country some review of the range of ecological work which is engaging those on the eastern seaboard. With this objective in view authors were selected whose interests covered rather varied aspects of oceanic phenomena. It would have been difficult to arrange a substantial program following the more usual procedure of focussing discussion on a specific and restricted problem because of the limited number of persons working on any one aspect of marine ecology, a difficulty enhanced by the fact that many of those who might have been called on have been otherwise engaged during the war and are not in a position to contribute new material.

The symposium opened with a review of the geochemistry of the ocean by Dr. G. E. Hutchinson which provides some glimpse not only of the origins of the conditions which characterize the marine environment but also of the interactions between the sea, the atmosphere, the land and the terrestrial waters. Thus this contribution provides a prospective on the more limited bodies of water found on land.

The phenomena considered by Dr. Hutchinson are primarily large scale events of a physical and chemical character. In the second paper Dr. B. H. Ketchum reviewed the more immediate interactions of marine organisms and the chemical components of their environment. The biochemical cycles involved are in principal identical with those which control organic productivity in lakes, rivers, and on land. In the sea the differences are those of scale and are particularly associated with the greater volume of deep water in which heterotrophic processes alone take place and the special part which the characteristic movements of sea water play in restoring plant nutrients to a biologically available position in the photosynthetic zone at the sea's surface.

If Dr. Ketchum's paper may be considered to review the relations of chemical and hydrographic factors to the abundance of life in the sea, the following contribution by Mr. W. E. Herrington presents the purely biological relationship between predator and prey; particularly its effect upon the abundance of the latter. In this case the prey is the most important commercial fish of the north Atlantic Coast, the New England fishing fleet is the predator. Mr. Herrington consequently presented a paper which not only illuminates a particular facet of the ecological system, it also gives a picture of the modern approach to applied fisheries ecology.

Of the purely physical factors which determine the distribution of marine organisms, temperature is without doubt the most significant. The paper by Dr. L. W. Hutchins presents a somewhat novel synthesis of the data bearing on this relationship. While the theory presented is based upon the distribution of oceanic temperatures and the geographical ranges of marine animals, the fundamental physiological concepts are applicable wherever, on land or sea, marked seasonal changes in temperature are encountered. Parenthetically, this paper is the outcome of an investigation initiated in the immediate interest of the armed forces during the war, which fortunately has resulted in a concept of much wider interest than its immediate objective.

The final review by Dr. T. C. Nelson deals with the ecology of the margin of the sea. This is the region where man most closely impinges on the ocean, and where it, in turn, most immediately affects his interests. It was thoroughly explored by the older naturalists, but the complexities inherent in the interaction of land and sea have discouraged both the oceanographer, who has preferred to investigate the simpler large scale phenomena of the open sea, and the limnologist, who finds the circumscribed volume of a lake more amenable to exact measurement. Nevertheless, Dr. Nelson has presented many suggestive observations which point the direction which important advances in marine ecology may be expected to take.
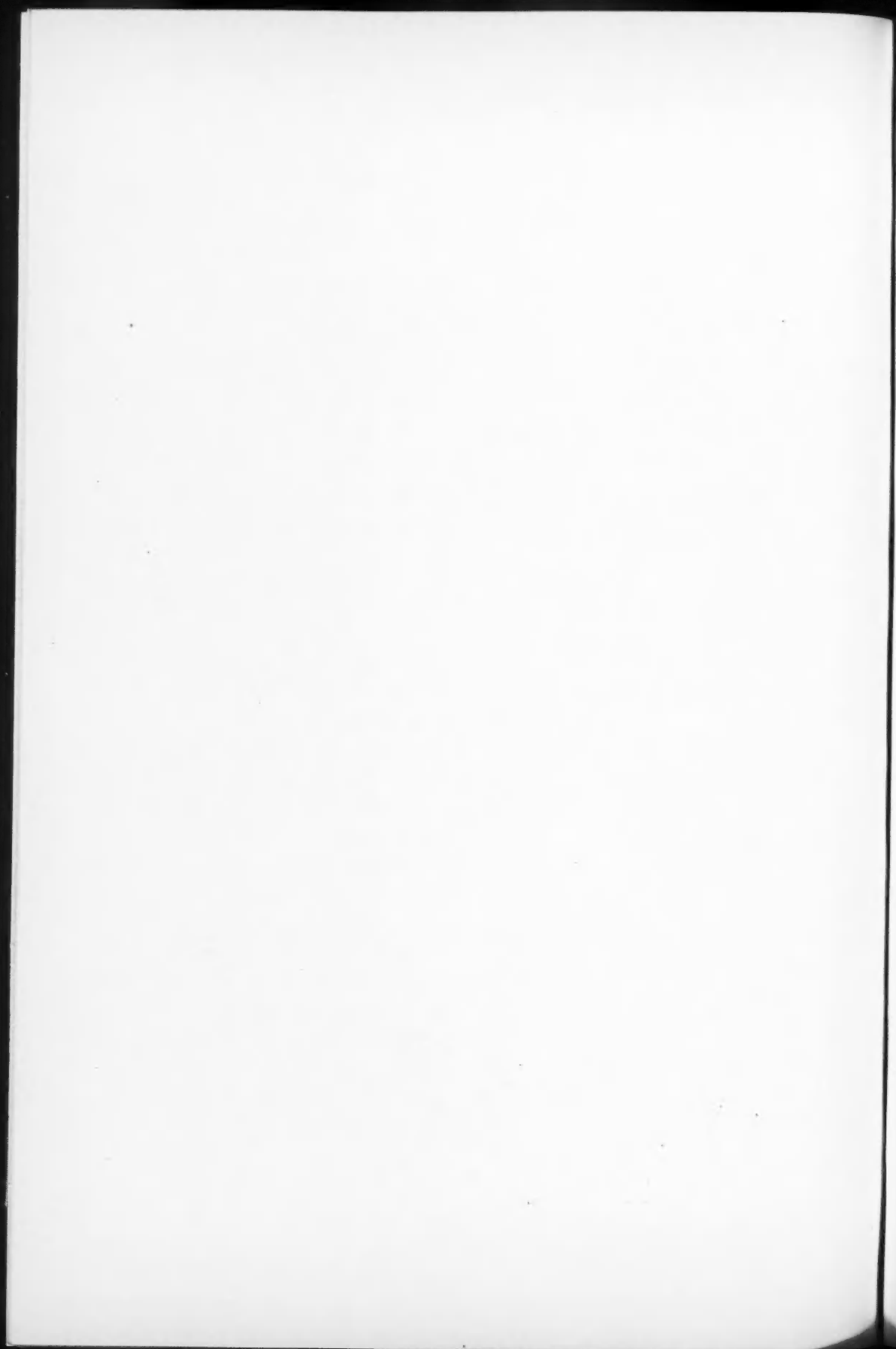
THE PROBLEMS OF OCEANIC GEOCHEMISTRY

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It may appear presumptuous for a limnologist to open a symposium on the ocean, and in doing so to treat of the most grandiose phenomena, occurring on a planetary scale. The only excuse for this behavior is that the limnologist is more accustomed to consider capacity factors than is the oceanographer. The labor and expense of obtaining adequate data for even a single deep station in the ocean is so great that the oceanographer has to be content with what always seems an inadequate number of observations. He seldom feels justified in extrapolation of his findings to the entire volume of the seas of the world. The limnologist, though actually he may have relatively no more data than the oceanographer, can when taking a station on all but the largest lakes, see the shore around him, and is tempted to consider the volume of his lake as a unit. The type of geochemical problem which is to be discussed in the present contribution is definitely best considered in terms of the volume of the entire ocean, in a manner to which the limnologist is particularly accustomed.

ANIONS AND WATER

It is hardly necessary to point out that the ocean consists of salt water. The geochemical history of the water raises the first and most difficult problems to be encountered, but it is best deferred until the salt is considered. The dominant component of the salt is of course sodium chloride, but the other alkalies and alkali earths are present as cations, and small amounts of the other halogens and considerable amounts of the complex anions. It is a remarkable but well established fact that the history of the cations, of say the sodium of common salt, is entirely different from that of the anions, say the chloride of the same salt.

There can be no doubt that the cations have ultimately been derived from the weathering of primary rock. Sodium alone is retained in solution in quantity commensurate with the amount delivered. Potassium is removed in the formation of clays and shales, which are about as rich as igneous rocks in the element, but are deficient in sodium, as is to be expected. The quantity of calcium and magnesium to be found in the ocean is at any time regulated by the solubility of their carbonates but Conway (1943) has pointed out that the removal of potassium by shales removes a base that is competing for chloride with the other bases. If suddenly any further amount of potassium were removed from the ocean to the sediments, the process would result in liberation of the equivalent amount of HCl in the ocean, which would dissolve calcium carbonate from the sediments. Conway thinks that the formation of the clays which remove potassium, is a biogeochemical process, and that removal of potassium with liberation of calcium actually occurred in this way during the pre-Cambrian when living organisms were first evolving. This attractive hypothesis provides a mechanism for a progressive increase in calcium until the Cambrian when calcareous shells appear. The evidence either for or against the hypothesis is at present inadequate, but further study of the most ancient sediments should throw light on the matter.

The history of the anions is very different for there is certainly not enough chlorine, bromine, iodine, sulphur, carbon or boron in the primary rock from which the sodium has been derived to supply the ocean with these elements.

In the first column Table 1 are set out the quantities of elements forming the chief anions found in sea water, referred arbitrarily but conveniently to unit area of Earth's surface. The total figures for the entire Earth can easily be derived approximately by multiplication by 5×10^{18}. In the second column are given the amounts of the same substances that have been lost to sedimentary rocks during the course of geological time, while in the third column is given the quantity that could have been derived from the primary rock that has been eroded to form the sediments.

TABLE 1.

Data from Goldschmidt 1938, with corrections for boron by Landergren (1945) and for carbon by Hutchinson (*in Press*).

In Ocean		Lost to Sediments	Total amount that has passed through biosphere	Derived from igneous rock	Derived from other sources
Cl.	5365 gm per cm².	?	5365 +	82	5283 +
C	5.5 " " " .	c. 3300	c. 3306	51	c. 3255
S	245 " " " .	310	555	80	475
B	1.2 " " " .	c. 20	c. 21.2	0.5	c. 21

Two features of this table are of significance. Firstly, the ratio of the anion retained in solution to that incorporated in the sediments is very variable, probably nearly all the chloride is retained, but nearly all the carbonate precipitated. Secondly, in every case the total quantity of the anions that is or has been

in the ocean is vastly greater than the amount that could be supplied by the weathering of igneous rock.

This great excess can receive two alternative extreme explanations; either it represents an excess of anions, present as acids, in the original ocean (hypothesis of original reserve) or it represents the results of additions of the anions from volcanic sources throughout geological time (hypothesis of continuous addition). Any cne of the infinite number of intermediate hypotheses are of course possible. The problem has been discussed by a number of authors for many years, and as will be indicated below, it is of immense importance in any consideration of the possible modes of origin of terrestrial living matter.

If it can be shown that the existence at some remote time of the anion under consideration in quantities of the same order of magnitude as that given in column 2 of Table 1 is inconsistent with the occurrence of processes known to have taken place at that time, and if it is possible to show that continuous liberation of the anion is not inconsistent with processes now occurring it will be evident that some hypothesis near that of continuous addition is more probable than an hypothesis near that of original reserve. This is about as far as it is possible to go at present.

The best case is provided by carbonate, because here the hypothesis of original reserve implies a *progressive change* in the composition of the atmosphere. The total quantity of CO_2 which appears to have circulated through the biosphere, and which on this hypothesis was originally present, is about 12,000 gr. per cm^2 of Earth's surface, which would exert a pressure of 12 atmospheres. CO_2 must have been continually extracted to form the limestones and the supply must now be all but depleted. There is very little doubt that this gloomy conclusion is incorrect. Conway has pointed out that, assuming a regular rate of deposition of the calcareous sediments, the atmosphere in Jurassic times would still have contained 5% CO_2, which seems to provide a most unlikely environment for the birth of the mammals. During pre-Cambrian times limestones probably produced as algal reefs in shallow inland sea are known. It is difficult to understand how such could have been formed or preserved under the great partial pressures of CO_2 that would have been present on the basis of the first hypothesis.

If we reject the extreme hypothesis of original reserve and turn to the hypothesis of continuous addition, we find that, assuming an age for the atmosphere of 3×10^9 years, the mean volcanic output of CO_2 will be 4γ per cm^2 per year. The latest value for the age of the Earth is about 3.3×10^9 (Holmes 1947). Smaller values have freely been used in geochemical calculations. The early history of our planet is so obscure that Holmes' value may well be excessive for the atmosphere. The value used above, however, seems reasonable. In Table 2 are given the extreme and mean values of the components by volume in samples of gases collected from Mauna Loa by Jagger, and regarded by Shepherd (1938) as "the

only satisfying collection of volcano gases that has ever been made."

TABLE 2.

	Minimum	Maximum	Mean
CO_2	1.42	47.68	14.07
CO	0.00	1.46	0.40
H_2	0.00	0.96	0.33
N_2	0.68	20.01	5.41
A (and other inert gases)	0.00	0.66	0.18
SO_2	0.01	13.57	5.68
S	0.00	0.25	0.10
SO_3	0.00	5.51	1.92
Cl_2	0.00	4.08	0.46
H_2O	36.18	97.09	70.73

CO_2 appears to be an important constituent of these gases; if the quantities are recomputed as masses instead of volumes the ratio of $CO_2 : H_2O$ is 81 : 100. Carbon dioxide is also well known as a significant component in volcanic emanations elsewhere. While the composition of such gases raises no qualitative difficulty to the acceptance of the hypothesis of continuous addition, it is extremely difficult to get any idea of whether such an hypothesis is quantitatively possible. The following considerations at least seem to suggest that the hypothesis may prove acceptable on quantitative grounds, though later it will be necessary to introduce a warning on the acceptance of any modern vulcanological data.

Verhoogen (1946) concludes that the total lava extruded since the beginning of the Cambrian cannot exceed a volume of 3×10^{22} cm^3, or adopting a reasonable density of 3.3, a mass of 10^{23} gms. This estimate may be too low, because it does not appear to include submarine volcanic activity. Assuming that the period since the opening of the Cambrian represents about one sixth of geological time, this extrusion of magmatic material would have to be accompanied by emission of 10% of its mass of CO_2, which seems to be by no means impossible.

If modern data, derived from a period that is admittedly volcanically more active than has usually been the case, are used, the amount of CO_2 that must be liberated per year per unit mass of magmatic material is found to be correspondingly less. Thus, according to Sapper (1927), approximately 382 km^3 of rock have been added since 1500 A.D. to the superficial lithosphere from volcanos, no allowance being made for generally distributed volcanic ash, which may well be negligible, or for submarine volcanic ejecta, which are probably of considerable quantitative importance. Allowing a density of 2, which may be a little too great owing to the porosity of many deposits, but which will tend to counterbalance material omitted in Sapper's estimate, the rate of ejection would be 1.86×10^{15} grms per year or 37γ per cm^2 per year. The 4γ per cm^2 per year given above thus would correspond to about 1.1% of the mass of volcanic rock now being ejected from volcanos.

It therefore appears that for the carbonate of the biosphere, an original reserve of 12,000 grms per cm^2 is very improbable and the events at the surface of the earth, though inadequately known are not hopelessly inconsistant with the hypothesis of continuous addition. It is indeed unlikely that any recent author has seriously admitted the hypothesis of an original reserve of 12 atmospheres of CO_2; the alternative volcanic hypothesis appears to be universally accepted. For the other elements it is unfortunately less easy to gain any adequate information.

There is at present no way of ascertaining whether the quantities of chloride or of sulphur compounds implied by the hypothesis of original reserve are inconsistent with existing geological knowledge. There are, however, data for the emission of both elements from one volcanic area, namely the Valley of Ten Thousand Smokes, Katmai, Alaska, studied by Zies. In Table 3 the estimates given by Zies (1929) of the annual liberation of these elements into the atmosphere are compared with the quantities that would be needed to account for the excess of the two elements indicated in the last column of Table 1, assuming that the process occurred regularly for 3×10^9 years. In both cases the quantity emitted by Katmai is a large fraction of the required amount. As Zies points out, many other volcanic regions are continuously emitting both elements, so that if we can assume that the chlorine and sulphur of Katmai are primary, these estimates are perhaps excessive, even on the hypothesis of continuous addition. Zies concludes that the very high ratio of F:Cl in the Katmai emanations indicates that their halogens are not derived from sea water. This is certainly reasonable, but, as is indicated below, the possibility of the major part of the steam and its acid gases being derived from sedimentary rock assimilated by the Katmai magma cannot be overlooked.

TABLE 3.

	Output from Katmai	Amount Required
Cl	1.24×10^{12} gm per year	8.8×10^{12} gm per year
S	0.28×10^{12} gm per year	0.8×10^{12} gm per year

The borate content of sediments has been investigated by Goldschmidt & Peters (1932), by Landergren (1945) and by Sahama (1945). The first named authors consider that there is an increase in boron content of argillaceous sediment with increasing age. They suppose that the original reserve in the ocean was high and that the older sediments were, therefore, more favorably placed for the accumulation of boron. Landergren finds that so far as Palaeozoic and later rocks are concerned the rise in boron content observed by Goldschmidt and Peters is illusionary. He obtained evidence that the boron content of modern marine argillaceous sediments depends in a linear manner on the salinity and so probably on the boron content. Landergren accepts the hypothesis of

a high original reserve of borate in the sea. Since the amount lost in sediments is apparently dependent linearly on the concentration, the concentration will at first fall exponentially, but later will reach a steady state value as boron derived from the erosion of uplifted sediments balances boron lost to the sea bottom. He supposes that the steady state was established by the beginning of the Cambrian. He analyzed two groups of pre-Cambrian sediments from Sweden. The less metamorphosed group is low in the element and is supposed to be of brackish water origin or to have lost boron during metamorphism; the more metamorphosed group is high in boron, which is supposed to be primary and derived from an ocean relatively rich in the element. Sahama, however, has also given a number of determinations of the boron contents of very ancient sediments. He obtained evidence that boron might be present in tourmaline derived from the parent igneous rock, but that in some cases additional boron was associated with tourmaline crystals formed after the sediment was laid down. This additional fraction was presumably of marine origin. None of his values for ancient argillaceous sediments, which range up to 0.01% B_2O_3, are as high as the highest given by Landergren. In general the boron contents of these very ancient sediments seems to be comparable to that of Jurassic and modern marine sediments. It does not, therefore, appear necessary to assume that the Archaean ocean was abnormally rich in the element though the difficulties of interpretations presented by pre-Cambrian materials are notorious.

The preceding paragraphs point to a continuous volcanic source for the carbonate and borate of the ocean, and less certainly for the chloride and sulphate also. Volcano gases and the ocean have moreover a major constituent in common other than compounds of the elements hitherto considered. This constituent, which forms the greater part of both bodies, is of course water. If it is necessary to admit that volcanic activity is the chief source of the major anions in the sea, it is obviously necessary to ask what fraction of the water of the ocean is of like origin. The results of such an inquiry are curious, and though they tend to cast doubt on much of the previous discussion, they suggest possible methods of investigation which might produce results of great value.

The mass of the water of the ocean is about 1.35×10^{24} gm. or about 270 kg. per cm^2 of Earth's surface. Other water, notably the polar ice caps and the water in sediments, would raise this figure to about 1.4×10^{24} gm. To produce this body of water in 3.0×10^9 years would require the addition of 0.47×10^{15} gm. of water per year.

Verhoogén concludes that since the lava extruded since the beginning of the Cambrian is unlikely to have been accompanied by more than 10% of its mass of water, not more than 0.7% of the mass of the ocean can have been added since the opening of the fossil record. On this basis not more than 5% of the water of the ocean is likely to have been of volcanic origin. Verhoogen however seems to

doubt his own conclusion. Part of the trouble is due
to the difficulty of accounting for the existence of
any water (mol. wt. 18) in or on the earth, seeing
that neon (mol. wt. 20), a cosmically common gas,
has almost disappeared. The interested reader is
referred to Verhoogen's very stimulating paper for
further details of the difficulties inherent in any
attempt to account for the existence of the ocean.
Nevertheless, as Verhoogen reminds us, the ocean does
exist. Even if the high rate of recent volcanic ejec-
tion had been continued throughout geological time,
which is most improbable, Sapper's estimate would
imply that the rock ejected would have to be accom-
panied by water vapor equal to 25% of its mass in
order to produce an ocean in 3×10^9 years. This
seems improbably high, though within the range be-
lieved possible by some vulcanologists. If, however,
we consider the one volcanic area for which quantita-
tive data are available, we obtain a most surprising
result. Zies estimates that in the Valley of Ten Thou-
sand Smokes, 26×10^6 litres of steam are emitted
per second. The density of steam at 100° C and
760 mm. being 0.5974 gm. per litre, this emission
corresponds to $26 \times 10^6 \times 0.5974 \times 365 \times 24$
$\times 3600$ gm. or 0.49×10^{15} gm. per year. Thus it
appears that the continuous existence of a single
volcanic source throughout the whole of geological
time, emitting as much water as did the Katmai
region at the time of Zies' study, would be sufficient
to account for the existence of the ocean.

This result, indeed, seems so fantastic that it is
difficult to take it seriously for, at least at the present
time, the total water vapor emitted by the volcanos
of the world must be much more than that emitted
by the fumaroles of the Valley of Ten Thousand
Smokes. Zies' argument against a direct marine
origin of the halogens on the grounds of the high
F:Cl ratio would presumably apply to the water
as well, particularly in view of the fact that the
steam at Katmai contains much less chloride (0.25%)
than does sea water. Atmospheric precipitation may
account for much of this water. It is, however,
conceivable that at least part is derived from the
essential water of clay minerals and other materials
in sedimentary rock assimilated by the magma. Fen-
ner's (1926) account of the region does not appar-
ently exclude the occurrence of such processes. If
they have occurred, it is not impossible that chlorine
and fluorine have been derived from the same sedi-
mentary source as produced the water, for the ratio
F:Cl is likely to be higher in sediments than in
the sea.

It is evident that until it is known how much of
the steam emitted by volcanos is primary non-cyclical
water the problem cannot be solved. The only way
in which any further information on this matter is
likely to be obtained is by an intensive study of the
isotopic ratios of the hydrogen, oxygen and carbon
in volcanic gases. Since, at least in the cases of the
oxygen of sea water and the carbon of carbonate
sediments, there is an enrichment in the heavier
isotopes O^{18} and C^{13} over the amount found in

primary rocks, it might be possible to gain some
idea of the sources of the volcanic emanations by
a study of isotopic ratios. Carbon would probably
be more indicative than oxygen because the oppor-
tunity for equalization of the ratio by exchange re-
action with primary materials would presumably be
less. Such a research would be in accord with the
suggestion of Kamen (1946) than an accurate and
extensive study of isotopic ratios could become a
powerful method of geochemical research. Until
such methods have been applied to volcano gases, it
is impossible to draw any certain conclusions as to
the history of either the anions or the water of the
ocean. Though the hypothesis of continuous addi-
tion seems adequate for carbon dioxide and perhaps
for borate, it is difficult to understand how it can
apply to water, but also difficult to see how the
atmosphere of the cooling earth could have contained
gases less dense than neon or why water and carbon
dioxide should behave in such very different ways.
It is, however, desirable before leaving the problem
to emphasize its immense interest. If the water of
the ocean is to be regarded as a bequest from the
earth's original atmosphere, it is impossible to avoid
the conclusions that the gases dissolved in the ear-
liest ocean included oxygen. Tamann (1924) has
pointed out and Wildt (1942) has further empha-
sized that, if the ocean were volatilized and raised
to a temperature of several thousand degrees, as
must have been the case before the solidification of
the lithosphere, oxygen and hydrogen would be
formed by dissociation, the former gas being retained,
the latter lost to space. Living matter would thus
have come into existence under oxidizing conditions,
protected from ultra-violet light by an ozone screen.
If the ocean were added gradually, which seems
probable on purely physical grounds, the initial at-
mosphere might have been devoid of oxygen and
short-wave ultra-violet might have penetrated to the
upper layers of the first shallow seas. The latter
rather than the former condition seems to the present
writer more likely to have provided the conditions
necessary for the origin of life. The most plausible
way to approach this most fascinating and seemingly
insoluble problem of biology is to ascertain as ac-
curately as possible the ranges of the ecological
variables that could be realized at the surface of the
newly solidified earth and then to construct, either
ideally or experimentally, models that might throw
light on what happened. The first difficulty that is
encountered is the question of oxygen, and this is
clearly linked with what really happens at the Val-
ley of Ten Thousand Smokes.

MANGANESE ON THE OCEAN FLOOR

It has long been known that manganese nodules
are scattered over many parts of the ocean floor, and
that some samples of red clay are particularly rich
in the element. When the ratio of MnO to Fe_2O_3
in the mean red clay is computed it is found to be
of the order of 5-10:100. This high ratio has puzzled
many investigators as there is no source material

likely to give such a high proportion of manganese. Kuenen's (1941) computation of the composition of the source material of the oceanic sediments indicates an expected geochemical ratio of 2.08:100. The problem has been recently discussed by Petersson (1945), who however comes to no conclusion. Unfortunately, Petersson evidently did not know of Kuenen's contribution in which the latter author suggests that the problem is illusionary. Kuenen points out that manganese is apparently precipitated at surfaces very slowly, but independently of other mechanically sedimented constituents. Ideally in making a composite sample of red clay, each individual specimen should be weighted according to its sedimentation rate. In practice this is usually not known, and each sample is, therefore, given equal weight. The equal weighting results in an over-representation of those sediments which form very slowly. If a region be imagined in which no mechanical sedimentation occurred, the only sediment represented would be the chemically precipitated manganese film, which would be immensely over weighted if equal masses of sediment were taken in making a composite sample. Inclusion of a few specimens rich in MnO would give an impossibly high MnO: Fe_2O_3 ratio.

Histograms showing the distribution of the variation of MnO per 100 parts of Fe_2O_3 in the deep water sediments of the tropical Atlantic are given in Figure 1. The data are derived from Correns (1937) and relate only to core samples collected at depths in excess of 2000 m. of water. In the top histogram all the analyses given by Correns are used; in the middle histogram only those from the tops of cores; in the lower histogram only those from the bottoms of cores. All three diagrams clearly represent the same type of distribution. It will be observed that in all three cases the majority of values cluster around the expected geochemical ratio, but that there are also a restricted number of specimens very high in manganese. Since in a series of samples of sediments, which might be supposed to be formed by the mixture of a variable but usually large amount of a manganese-free material with a small constant amount of MnO, the zero ratio could not occur, it may be fairer to make use of a logarithmic or geometrical scale of categories. This is done for the entire series to the right of the figure; the resulting histogram naturally appears more symmetrical, but by inverting the part to the left about the line representing MnO :100 Fe_2O_3 = 2.5, it is easily seen that
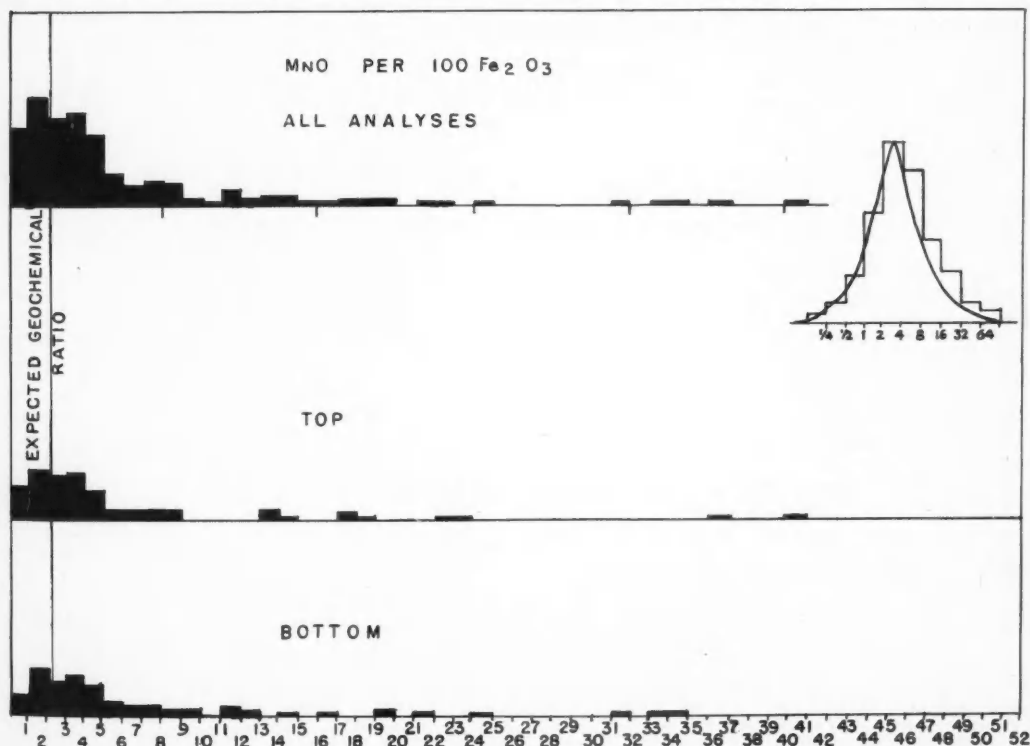
FIG. 1. Histograms showing the distribution of the ratio MnO/100 Fe_2O_3 in tropical Atlantic sediments from depths in excess of 2000 m. The upper section refers to all samples, the middle to material from the tops of cores, the lower section to the material from the bottoms of cores. Four samples are omitted from these arithmetic plots in order to keep the diagram within a reasonable width. Two of these omitted samples, with ratios of 66.2 and 73.0, belong to the series from the tops; two, with ratios of 75.2 and 79.6, belong to the series from the bottoms of cores. All four are included in the plot for the whole series, on a geometrical scale, given on the right.

the distribution is skewed in favor of the higher ratios. The general type of distribution indicated by these histograms clearly is in accord with Kuenen's hypotheses. A further study of the data, however, renders this hypothesis unacceptable, which perhaps might be expected, as it is clear that, at least in shallow water, manganese films can be deposited at different rates according to the environmental conditions (Murray and Irving 1895; cf. also Betekhtin 1944).

In the tropical Atlantic cores, Schott (1935) has shown that two layers containing the foraminiferan *Globorotalia menardii* usually occur, separated by a layer lacking this foraminiferan. The layer without *G. menardi* is taken to represent the last Pleistocene glacial period. The thickness of the upper layer containing *G. menardi* is thus a measure of the rate of post-glacial sedimentation. The chief constituent of many cores is the calcareous material of foraminiferal shells, which is irrelevant to the present discussion. A rough measure of the rate of non-calcareous sedimentation can be obtained by multiplying the thickness of the post-glacial layer by the fraction of the sediment that is not $CaCO_3$. Some error is introduced by the necessity of using the weight composition of the sediments rather than the volume composition. It is, however, reasonably certain that in those cases where the estimate of postglacial sedimentation is low, the actual deposition has taken place slowly, and where the estimate is high the deposition has been rapid. According to Kuenen's hypothesis, the ratio $MnO:100\ Fe_2O_3$ should be high in the former and low in the latter. Inspection of Figure 2 gives absolutely no reason for believing this to be the case. Since the MnO content and the ratio vary greatly from top to bottom in some cores, it might be argued that the surface values give little indication of the ratio throughout post-glacial time. The encircled dots represent all those cases where, considering the top and bottom of a core, the higher value is less than 1.5 times the lower, and in which, therefore, there is a fair probability of relatively uniform ratios throughout the core. The distribution of this restricted class of points is of the same type as that of the extended series. If anything but a random distribution is implied by this diagram it is that high ratios tend to occur in the middle of the range. It is obviously very difficult to reconcile these findings with Kuenen's hypothesis.

Considerable effort has been expended in an attempt to find some significant correlation between the MnO content referred to Fe_2O_3 and other variables in both mud and water. The only fact that
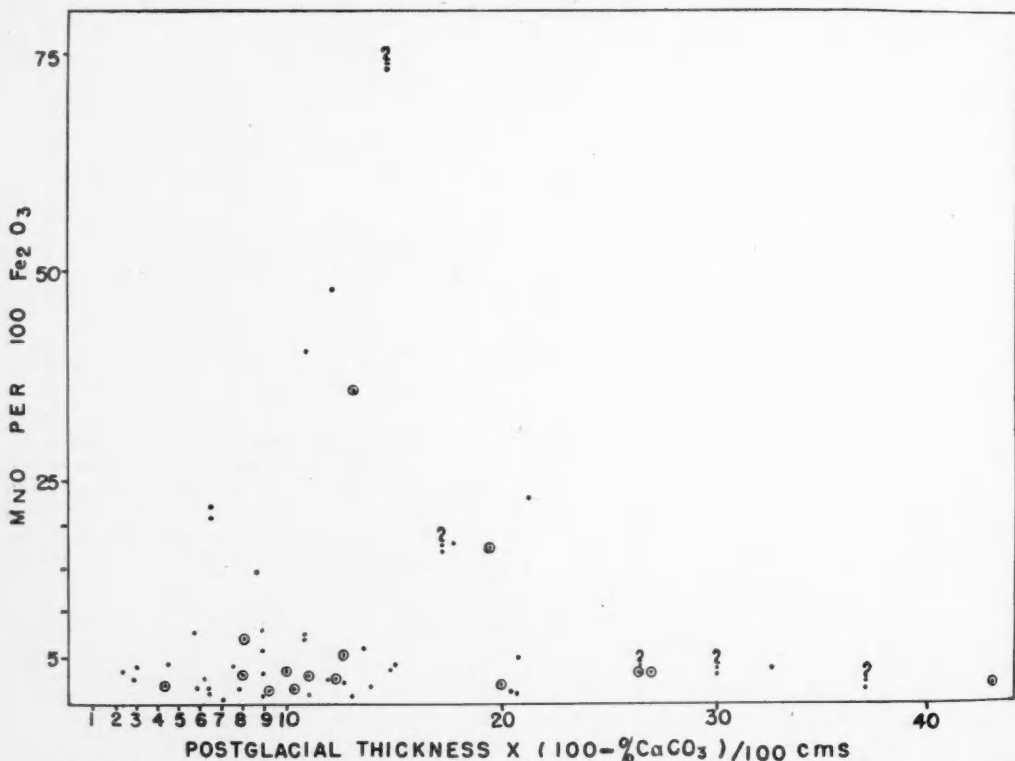
FIG. 2. The ratio $MnO/100\ Fe_2O_3$ for the tops of cores, plotted against a rough estimate of the postglacial thickness of the non-calcareous sediment. The circled dots refer to samples from cores in which the highest value did not exceed 1.5 times the lowest value. The ? indicates uncertain dating.

emerges is that the high and low values for the ratio tend to have a latitudinal zonation (Fig. 3). This zonation runs across the main orographic features of the floor of the Atlantic. It does not suggest any probable distribution of source materials of varying manganese content. It has clearly not been very constant in time, as can be seen in the figure in which the contour, enclosing points where the ratio from the bottoms of the cores in excess of 5, is also plotted. The latitudinal arrangement suggests that the manganese content of the sediments is more likely to be determined by events in the superficial layers than by events at the bottom. If this proves to be correct the distribution of manganese at different depths in cores is obviously likely to throw unsuspected light on the recent history of the ocean.

bird droppings, is also known on many elevated atolls throughout the Pacific. The phosphatized atolls on which existing bird colonies are responsible for the deposit are associated with a dry equatorial area, just south of the doldrums, and corresponding to a divergence in the Southern Equatorial Current.

In addition to these islands there are a number of old elevated coral islands which bear extraordinary quantities of phosphate. Nauru, Ocean Island, Makatea, Angaur and some of the Mariana and Daito Islands are the most striking examples in the Pacific. Christmas Island south of Java provides a case in the Indian Ocean, while Navassa, Sombrero and Curaçao are the three most striking examples in the Caribbean. The geological evidence is inadequate to date the phosphate deposits on these islands accu-
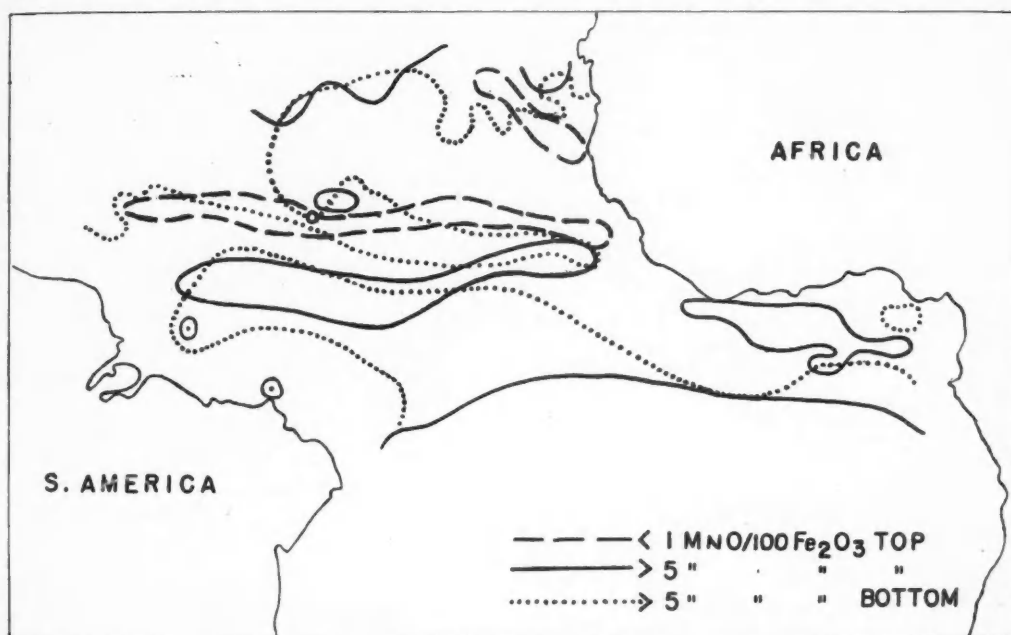
FIG. 3. Geographical variation of the ratio $MnO/100 Fe_2O_3$.

POSSIBLE INCREASES IN THE PRODUCTIVITY OF THE OCEAN DURING INTERGLACIAL PERIODS

The problems that have been discussed above are either concerned with the entry of certain substances into the ocean, or with the loss of substances from the ocean to the sediments. All such problems may seem somewhat remote from the economy of the seas as viewed by the biologist. The final example to be given is related to the central problem of the biological fertility of the ocean. It can here only be discussed in its broadest outline; a full and documented account will shortly go to press.

On certain islands, notably on the western coasts of the continents, immense numbers of birds deposit a correspondingly immense amount of excreta. Phosphate, derived from less striking accumulations of

rately, but they are certainly post-Miocene and pre-Holocene; no violence is done to the evidence by supposing all of them to be Pleistocene. The occurrence is of the same general pattern in all cases. The phosphate occurs in spaces between pinnacles of a Karrenfeld cut in elevated and often dolomitized coral rock.

The largest deposit is that of Nauru, where the original reserve was 87,500,000 tons of rock phosphate equivalent to about 14,900,000 tons P or 82.9 gms. per cm^2 of island surface. It is interesting to inquire into the time that was necessary to produce such a deposit. Of the equatorial islands which are oceanographically comparable to Nauru, Howland Island is the best known. It appears to have produced guano corresponding to about 18,400 tons P. The area of the island is 1.62 km^2 but only about

one half seems to have been phosphatized so that the original reserve corresponded to about 2.39 gm. P per cm^2. Comparison with Nauru therefore suggests that its deposit would have taken about 35 times as long to form as did that on Howland Island. Actually it is practically certain that the time taken would have been vastly greater. On Howland Island the bird colony must have occupied a very large part of the area within the rampart. Malden Island with an area about twenty times that of Howland certainly did not have a bird colony that covered the greater part of its dry surface, and it seems to have produced only about four times as much guano as did Howland. This is to be expected since the size of a breeding colony in an area of limited productivity presumably will depend on the area of ocean within cruising radius of the birds, which will be little increased by an increase in the size of the island. Assuming that the very imperfect information from Malden Island really indicates that the total quantity of guano that could be produced on a large island in the region of Howland is about four times that actually produced by the latter, it would seem that it would have taken about 14,900,000/4 × 18,400 or 200 times as long to produce the Nauru deposit as the Howland.

It is unfortunately difficult to ascertain how long the Howland deposit took to form. It must have accumulated entirely in post-Pleistocene times, and presumably during the course of thousands rather than hundreds of years. Evidence derived from the Peruvian coast suggests that a slight hydrographic change occurred in the Pacific at some period during the first or second millennium B.C. This is the most recent change that can be identified in the Pacific basin, so that it is reasonable to suppose that the Howland deposit was initiated at least 2500 years ago. Such a minimum age would suggest that, under modern hydrographic conditions, it would take half a million years to produce the Nauru deposit. Such an estimate would probably have to be reduced somewhat if Baker Island, which seems to have been rather more productive per unit area than Howland Island, had been used in the comparison, but the period required would still be of the order of hundreds of thousands of years.

In view of the rather critical conditions required for the contemporary phosphatization of raised atolls, which have accumulated over 100,000 tons of phosphatic material in post-Pleistocene times only in the limited area of the drier Line and Phoenix Islands, it is extremely difficult to understand how the requisite conditions could have persisted on Nauru for a large fraction of one of the most changeable periods of the Earth's history. Moreover, such evidence as can be assembled from the western Pacific strongly suggests that intense phosphatization was a transitory phenomenon that occurred on more than one occasion. It would, therefore, appear that at certain times during the Pleistocene the central Pacific was more productive than it is today, and that in general such periods corresponded to times of somewhat re-

duced rainfall during which previously dissected islands were bare enough to permit colonization by immense numbers of ground or rock breeding birds. The distribution of the major phosphatic islands in all the tropical regions where suitable islands occur furthermore suggests that this increased productivity at a time of low rainfall was due to causes operating on a planetary scale.

In the course of a discussion of other zoogeographical matters, my friend Dr. Ernest F. Thompson pointed out that if the polar ice sheets disappeared the whole thermal regime of the oceans would be altered, as there would be no major source of deep and intermediate cold water available at high altitudes. At least for a time after such an event there would be a marked increase in the circulating phosphorus and nitrogen of the ocean as the vertical thermal gradient was reduced and the immense stores of nutrient elements were liberated into the trophogenic layers of the sea. At the time of such a change much of the ocean might have reached a level of productivity comparable to that of the Peruvian guano coast, where deposits of the size of Nauru could have formed in the course of thousands rather than hundreds of thousands of years. If such an increase in productivity accompanied one of the major interglacial periods, the phenomenon of the great Pleistocene phosphate deposits throughout the world would receive a reasonable explanation. The hypothesis is at least of sufficient interest to justify intense study of the relevant localities, none of which are as well known as they should be. If the views that have been put forward are confirmed, the study of phosphatic islands should add considerably to our knowledge of the climatology and oceanography of the Pleistocene period.

CONCLUSION

The three problems that have been considered all involve concepts outside the ordinary domain of oceanography. They are not the kind of problem that biologists ordinarily feel called upon to solve. They are, however, in their genesis partly of biological origin and in their solution, if it is ever achieved, of immense biological implication. It is hoped that the somewhat speculative approach that has been adopted will be justified by bringing together biologists and geochemists in the study of some of the most obscure yet grandiose and significant events in the history of our planet.

My best thanks are due to Mr. V. T. Bowers for helpful suggestions on the manganese problem in the ocean.

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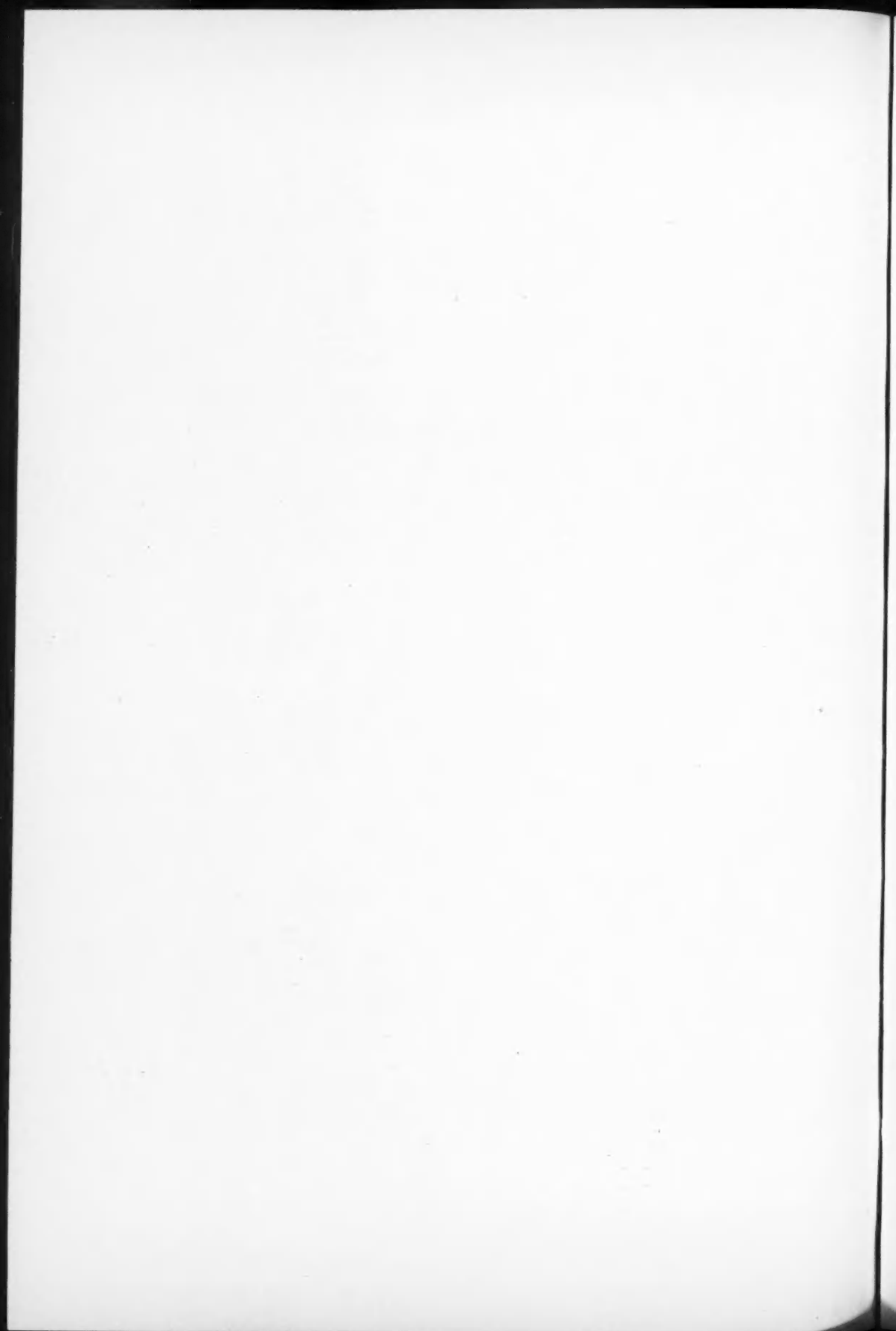
THE BIOCHEMICAL RELATIONS BETWEEN MARINE ORGANISMS AND THEIR ENVIRONMENT

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The chemical nature of an aquatic environment is changed by the growth and activity of the organisms which it supports. Photosynthesis by green plants removes carbon dioxide and essential plant nutrients from the water and adds oxygen and organic matter in the form of new living tissue. Decomposition, whether it results from bacterial action, or the respiration of plants and animals, removes organic matter and oxygen and replaces or regenerates the carbon dioxide and essential plant nutrients. These changes may proceed to such an extent that the lack of an essential element may ultimately limit the growth of the very organism which caused the deficiency. Before this extreme condition is reached, however, the changes in the environment may have a direct effect on the composition or physiological state of the organisms. Superimposed on these biological changes are the effects of the motion of the water itself which may transport new supplies of these materials into the area.

Three processes, therefore, must be considered simultaneously in order to secure a complete picture of the changes in the biologically active constituents of the water. These are the assimilation, due to photosynthesis, the regeneration, due to processes of decomposition, and transport, due to the motion of the water.

In the sea most of the elements essential for photosynthesis and plant growth are present in great excess. Available phosphorus and nitrogen compounds, however, are found in only small concentrations, and may be completely removed from the water by the activity of the plants which make up the phytoplankton population.

The assimilation of phosphate and nitrate from the water occurs at different rates, but their concentration in the water is such that they become exhausted at about the same time as a result of extensive phytoplankton growth. If the replenishment of these elements were negligible, plant growth in the surface waters would be at a standstill during a large part of the year. It is the rate of replenishment, and not the concentration observed at a given time, which determines the fertility of an aquatic environment. This replenishment is provided by the two processes of decomposition and water circulation.

The net result of the three processes is to maintain the ratio of phosphorus to nitrogen at a nearly constant value in the sea. Examples of the uniform ratio of these elements in the Atlantic, Indian and Pacific Oceans are given in Figure 1, which is reproduced from a paper by Redfield (1934). Though the concentration of nitrogen varies about 600 fold and that of phosphorus about 150 fold the ratio of their concentrations in the water is never far from 15 atoms of nitrogen to 1 of phosphorus.[2] A similar correlation will be found in this same paper between the changes in the carbonate and the nitrogen content of the water. The constancy of these ratios imply that the organic matter synthesized and decomposed in the sea will contain, on the average, about 16.7 grams of nitrogen and 2.5 grams of phosphorus for every hundred grams of carbon°. These ratios have proved useful, since it is often possible to compute, from observations of one biologically active element, the probable changes in others.

It is pertinent to inquire whether the constancy of these ratios in the sea is determined by the physiological properties of the organisms, and whether living matter produced under different nutritive conditions is uniform in composition.

Experiments on the assimilation of nitrate and phosphate during photosynthesis by the marine diatom, *Nitzschia closterium*, have shown that the rate of assimilation of phosphorus is related to the concentration of both phosphate and nitrate in the medium. The rate of assimilation of nitrate, however, is independent of the phosphate concentration and related only to the concentration of nitrate in the culture medium (Ketchum 1939a). In Figure 2 a grid is presented in which the phosphate concentration of the culture medium is plotted against the nitrate-nitrogen content. Any simultaneous change of these two nutrients is indicated by a line connecting the initial and final concentrations. If the rate of removal of phosphate is relatively great the slope of this line will be steep. If the rate of removal of nitrate is relatively high the slope will be more nearly flat. The lighter lines show the changes which may be expected in the media as predicted from observed rates of assimilation of nitrate and phosphate by pure cultures of *Nitzschia closterium*. The heavier lines show actual simultaneous changes observed in individual cultures of this diatom.

If the physiological activity of this diatom is typical of the action of the phytoplankton population a prediction of the effect of their activity on the com-

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[1] Contribution No. 377.

[2] These ratios have been corrected for the salt error of the phospate analysis as determined by Cooper (1938).
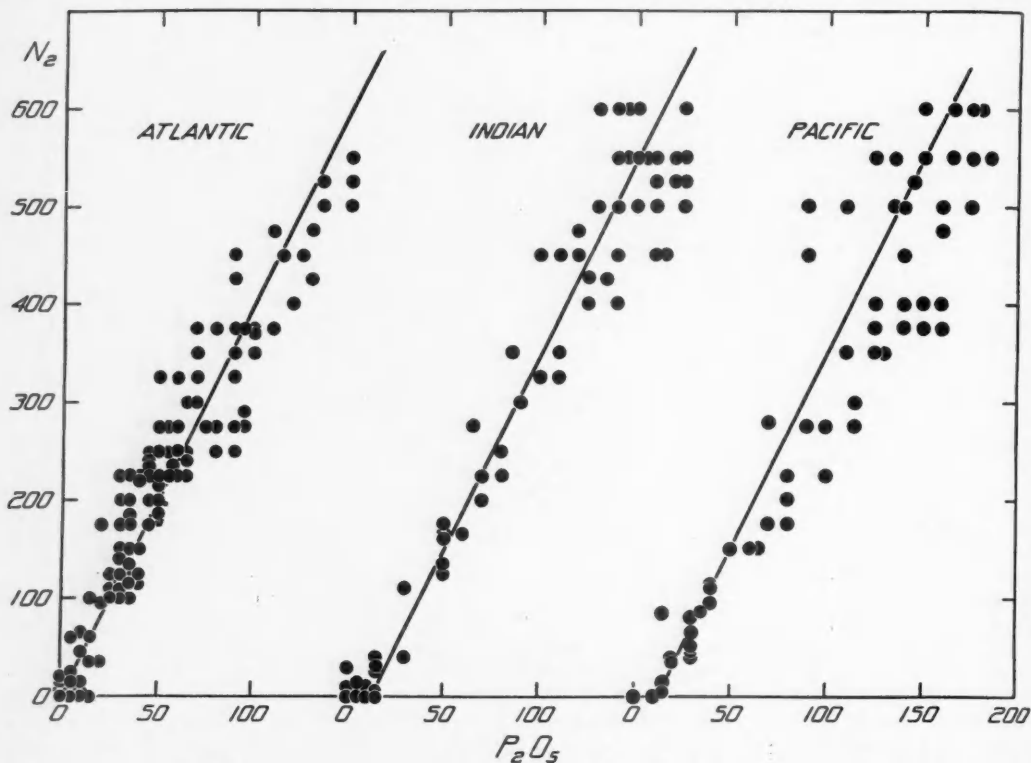
FIG. 1. Correlation between concentration of nitrate and phosphate in the waters of the Atlantic, Indian and Pacific Oceans. After Redfield, 1934.

position of the water may be made. The normal ratio of nitrogen to phosphorus in the sea would be represented in this figure by a line joining zero and the point described by a phosphate concentration of 100 and a nitrate-nitrogen concentration of 220. If
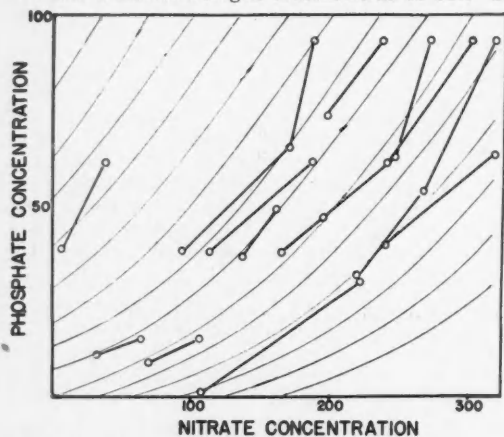

FIG. 2. The simultaneous removal of phosphate and nitrate from sea water of various compositions by the marine diatom *Nitzschia closterium*. Ordinate, gamma N per liter, abscissa gamma PO_4 per liter. After Ketchum, 1939a.

the phosphorus:nitrogen ratio in the medium is high the metabolism of the cells tends to change the ratio of the concentration in the water so that it approaches more closely the normal ratio. If, however, the ratio of concentration is low, due to a relative lack of phosphorus, the metabolism of the cells tends to increase the discrepancy.

The assimilation of these nutrients is an essential part of the synthetic processes which produce the organic matter which supports all life in the sea. It is essential, therefore, not to lose sight of the products of the syntheses and their variations with different environmental conditions.

Various analyses have been made of the carbon, nitrogen, and phosphorus content of both phyto and zooplankton. On the average, their composition closely resembles that of the sea water from which the nutrients were assimilated. The data are, however, far too incomplete to know whether there are consistent differences between species, or whether seasonal variations in composition of the plankton occur. Additional information on the composition of natural collections of planktonic algae is greatly to be desired.

Some indirect indications of possible variations can be obtained from analyses of pure cultures of algae. The carbon, phosphorus and nitrogen content of 6

species of algae which were grown in bacteria free cultures are shown in Table 1 (Ketchum & Redfield 1938; Ketchum, Lillick & Redfield Ined.). For each 100 parts of carbon the nitrogen content varies between 12.2 and 15.4 parts and the phosphorus content between 3.3 and 8.7 parts. These algae were grown in identical media and the observed variations in their composition are, consequently, not the result of any variations in their chemical environment. They may, thus, be attributed to the physiological differences in the species of algae studied.

TABLE 1. Composition of various fresh water algae grown in pure cultures.

Species	PARTS BY WEIGHT		
	Carbon	Nitrogen	Phosphorus
Stichococcus bacillaris...	100	13.8	3.33
Chlorella pyranoidosa...	100	12.4	5.87
Chlorella vulgaris.......	100	14.5	5.51
Scenedesmus obliquus...	100	13.8	8.73
Scenedesmus basilensis..	100	15.4	6.69

Variations in the composition of algal cells may also be the result of growth in an unbalanced medium. The data in Table 2 show that *Chlorella pyrenoidosa* grown in the absence of nitrate and phosphate in the medium developed deficiencies in these elements within the cell. When the medium is again enriched with these elements the cells are able to assimilate them rapidly to make up their deficiencies. This assimilation is not dependent upon photosynthesis, since it can also occur, though at a slower rate, in the dark. As would be expected, the cells containing the least nitrogen were grown under conditions where their phosphorus supply was ample but their nitrogen supply was restricted. Conversely, the cells containing the least phosphorus were grown in a solution containing an adequate supply of nitrogen but no phosphorus (Ketchum 1939a).

TABLE 2. Variations in the composition of *Chlorella pyrenoidosa* as the result of growth in media deficient in phosphate and nitrate.

Experimental Treatment	PARTS BY WEIGHT		
	Carbon	Nitrogen	Phosphorus
Normal *Chlorella* culture...	100	12.4	5.89
Deficient *Chlorella* culture .	100	5.9	2.12
Recovery, Phosphate added	100	4.0	3.76
Recovery, Nitrate added...	100	16.2	1.15
Recovery, both added.....	100	13.9	4.48

Since it is known that the nitrogen and phosphorus content of the sea water varies between wide limits during the period of phytoplankton growth it is possible that cells deficient in these elements may be produced. Further data are necessary, however, to show just how great the changes in natural populations may be. Until this is known it is not possible to calculate exactly the productivity of ocean waters by determining the quantity of nitrogen or phosphorus removed from the water by the growth of the phytoplankton.

The regeneration of the nutrients in the sea is the result of two major biological processes. The plants may be consumed by animals and a portion of the nutrients is then excreted either in organic or inorganic form. The bacterial regeneration of nutrients acts directly on the dissolved organic materials in the water or upon dead plant or animal tissues. The net result of these two processes is to return the essential elements to the water in a usable form. The nutrients regenerated in the surface water, where there is adequate light for photosynthesis, are directly assimilated, and start the cycle again. Those regenerated in deeper water must await transport to the surface by vertical water motion.

It has been impossible to duplicate the natural rates of bacterial decomposition in the laboratory. As soon as a sample of natural water is enclosed in a bottle an enormous increase in the bacterial population develops. The rates of regeneration under these conditions are clearly of little direct application to the conditions which obtain in the sea. The fundamental character of the changes, however, can be studied. It has been found, for example, that when glucose is added to sea water, it is oxidized by the bacteria, and phosphate and nitrate are removed from the sea water in the process. Large additions of glucose, therefore, require enrichment of the water with these elements if the oxidation is to be carried to completion. If complete plant or animal material is added, on the other hand, the ample supplies of phosphorus and nitrogen are present in organic form, and are liberated in inorganic form as a result of the decomposition (Waksman & Carey 1935, Waksman & Renn 1936).

Both phosphorus and nitrogen may be liberated first as soluble organic compounds. The availability of such materials for assimilation by the plant cells is not known. All of the inorganic compounds of nitrogen, however, are readily assimilated by the plant and there is some indication that ammonia, which is produced first in the decomposition of nitrogenous organic matter, can be assimilated somewhat more easily than nitrate or nitrite (Harvey 1940). The experiments of von Brand, Rakestraw and their collaborators (1937-1942) indicate that ammonia may be produced very quickly from particulate organic matter and this will be immediately available for assimilation. Under conditions in the sea the phosphate may be returned to the water more quickly than are the nitrogen compounds. The rates of these processes must influence the availability of these essential nutrients during much of the year at higher latitudes where the supply is seriously depleted during the summer.

In the study of the cycle of photosynthesis and decomposition in the sea, as evidenced by the essential nutrients, the three major processes mentioned above must be taken into consideration. To reiterate,

these are the assimilation by plants, the regeneration, either through animal excretion or bacterial decomposition, and the transport because of vertical or horizontal water movement. The relative importance of these three may be shown by the study of the distribution of phosphorus in the Gulf of Maine by Redfield, Smith, & Ketchum (1937).

The phosphorus content of the water was separated analytically into three fractions. These were the inorganic phosphate, the phosphorus combined in dissolved organic material and the phosphorus in particulate matter which could be filtered from the sea water. The distribution of each of these three fractions of phosphorus with depth in May and in November is shown in Figure 3. The inorganic phosphate is the form available for assimilation by the plants. The particulate phosphorus includes that in the microscopic living organisms, as well as any which may be present in detritus. The dissolved organic phosphorus is a step in the decomposition of the organic matter. The cycle of phosphorus is thus from inorganic to particulate to dissolved organic to inorganic.

During the interval between these two measurements a considerable accumulation of dissolved organic phosphorus occurred throughout the entire water column. The numbers on the right hand side of the figures show the percentage of total phosphorus found in each quarter of the water column. These show that the surface layer is somewhat depleted of phosphorus, and that little net change occurred between the two measurements.

In order to interpret and evaluate the changes which took place between these two measurements it is necessary to establish the direction in which changes are possible.

(1) The synthesis of organic matter, which changes inorganic to particulate phosphorus, can occur only in the upper layers of the water where there is adequate light for photosynthesis. The upper 60 meters probably closely defines this depth, and is called the surface layer.

(2) Transport of phosphorus downwards can occur only in the particulate form by the sinking of dead and dying organisms.

(3) Vertical transport of phosphorus upwards can occur only as a result of eddy diffusion of inorganic phosphate across the concentration gradient in the upper water layers.

(4) Decomposition of particulate to dissolved organic, and from the latter to the inorganic form can take place at any depth in the water column.
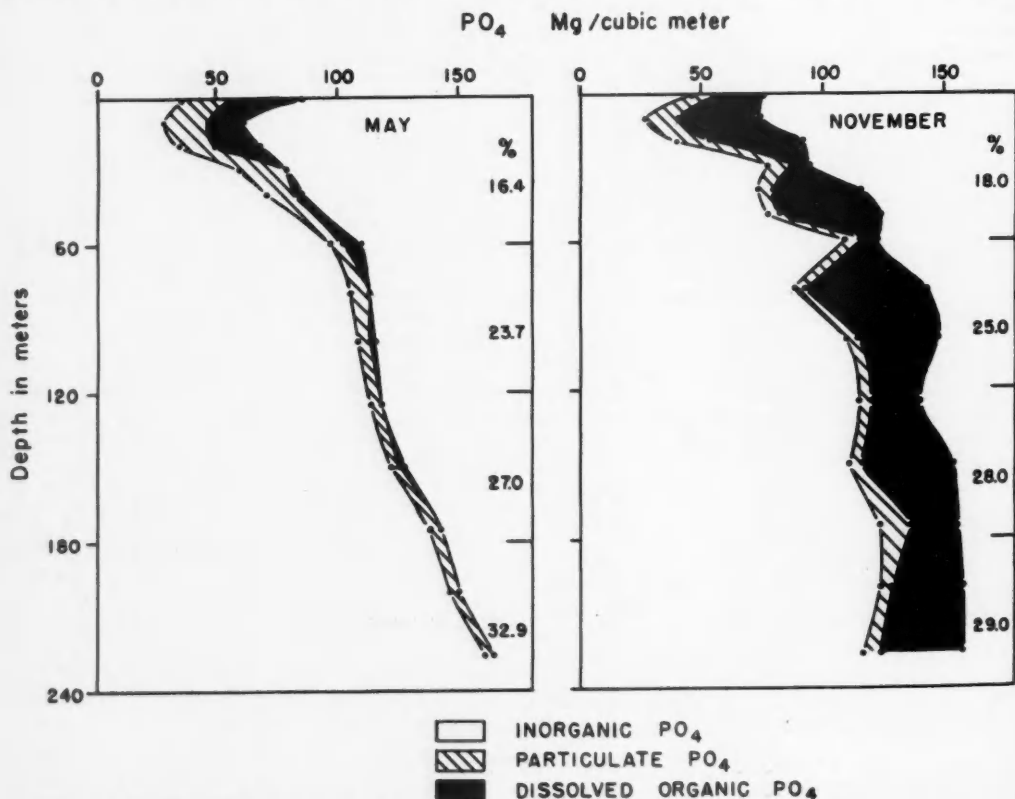
FIG. 3. The distribution with depth of inorganic, particulate and dissolved organic phosphorus in May and November in the Gulf of Maine.

In addition to these conditions which determine the direction in which the changes can occur it is also necessary to assume that horizontal transport may be neglected. This is never strictly true, and is approximately true only if the location is surrounded by a large area of similar water. The properties of a closed system have been artificially imposed upon our observations, however, by calculating all changes as percentages of the total.

The seasonal variation in the three fractions of phosphorus in the surface layer are shown in Figure 4. The period we are considering, between May and November, is the period of greatest photosynthetic activity, when inorganic phosphate is depleted in the surface waters. Even in midsummer, however, the total phosphorus in the surface layers is a substantial part of maximum amounts ever found there, though it is mostly present in combined organic form. The lower part of this figure shows the distribution of phosphorus with depth throughout the year. The phosphorus in the upper quarter of the water column varies from about 15 to 22% of the total phosphorus. When all of the fractions of phosphorus are considered, therefore, it is clear that the surface layers at this location are never exhausted of this nutrient, though a large proportion of the supply is combined, and is not available for assimilation by the plants. The conversions and rate of supply of available phosphorus must determine the fertility of the region.
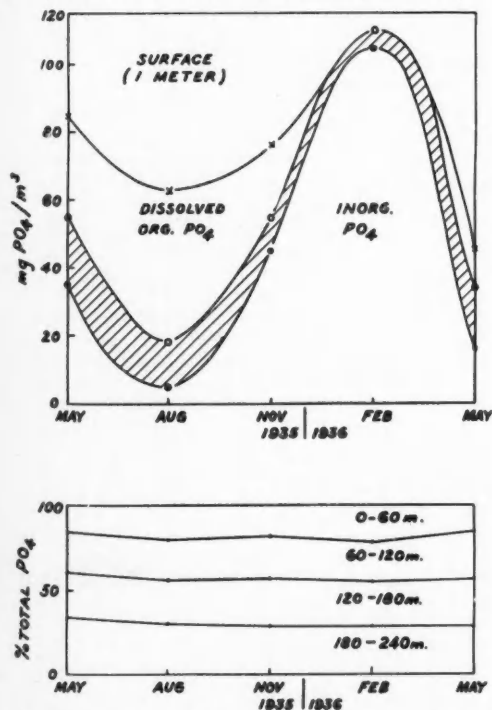
FIG. 4. Above: The seasonal changes in inorganic, particulate and dissolved organic phosphorus in the surface waters of the Gulf of Maine. Below: The proportion of total phosphorus in each quarter of the water column throughout the year.

The net changes in total phosphate between the May and November observations are small. There was a net gain of only one-half a gram of phosphorus by the surface water and a net loss of one-half a gram by all of the water below 60 meters. The total changes in the various fractions of phosphate are diagrammed in Figure 5. The deeper waters have gained more than 5 grams of organic phosphate most of which appears in the dissolved organic form. This must have been contributed by the sinking of particulate matter into this zone and its subsequent partial decomposition. To compensate for this gain there has been a slightly greater loss of inorganic phosphate. Since inorganic phosphorus can be utilized in synthetic processes only in the surface layers this must have been carried upwards in inorganic form by eddy diffusion and mixing. It was not found, however, in the surface layer which actually showed a slight decrease in inorganic phosphate during the same period. It must, therefore, have been assimilated by the plants and synthesized in organic matter.

<div align="center">(Units, grams PO₄/m²)</div>

(Units, grams PO_4/m^2)
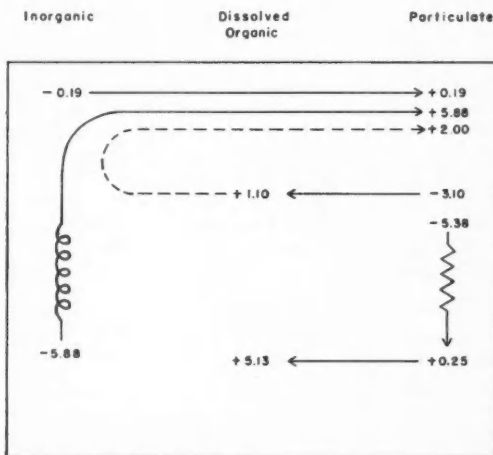
FIG. 5. Diagrammatic presentation of the conversion of phosphorus in the Gulf of Maine between May and November.

There is no direct way of measuring the amount of decomposition and regeneration of organic material which occurred in situ in the surface layers. There was, however, an increase of more than a gram in the amount of dissolved organic phosphate in this layer and this must have been derived directly or indirectly from the particulate material. In order to complete the picture an estimate has been made of the amount of material which may have completed the cycle of decomposition and re-assimilation in the surface layer. This estimate is based upon the rate of decomposition which was observed during the hundred days following the November observations when plant activity was at a minimum. At the end of this time, in February, it was found that a con-

siderable decrease in organic phosphorus compounds had occurred throughout the water column with a compensating increase in inorganic phosphate. The rate of disappearance of the organic phosphorus observed in the upper 60 meter layer was 11.5 milligrams per day. This corresponds to a regeneration during the period of May to November of two grams. Although this estimate is obtained indirectly it is probably nearer the truth than to postulate that no decomposition took place within the layer because that part of the cycle which has gone to completion cannot be detected.

The fact that part of the cycle which has gone to completion is lost results in minimum estimates for the various changes in the cycle. For example, the effect of adding a quantity X to any step of the cycle results in no change in the net gains and losses of the system so long as the quantity, X, is carried through the complete cycle of vertical transport, synthesis and decomposition.

That the quantitative aspects of the cycle are not unduly under-estimated, however, can be shown by comparison with other results which were obtained by different methods. Seiwell (1935) calculated the production of organic carbon in the tropical Western North Atlantic to be 278 grams of carbon/sq. meter/year. This calculation was based on the assumption that the oxygen minimum layer of the mid-Atlantic is caused by the oxidation of organic matter produced in the overlying water. Redfield (1942) has shown that a considerable part of the oxygen is utilized in the oxidation of organic matter formed at the surface in higher latitudes. Seiwell's estimate of local production is thus too high. Seiwell estimated that the plankton produced would require the vertical transport of 7.56 grams of phosphorus. This would be equivalent to 20.8 mg/sq. meter/day. Riley's (1941) figures for the organic production on George's Bank vary from 140 to 950 mg of carbon/sq. meter/day during a period from April to September. If one assumed a "normal" carbon to phosphorus ratio of 100:2.5 the phosphorus assimilation during this period ranges from 3.5-23.2 mg P/sq. meter/day. Our values of 10.3 for vertical transport or of 14.2 mg/sq. meter/day for total utilization are within these limits obtained by independent methods of estimation.

It is clear from this description that it is impossible to define the total changes which take place in one of the essential plant nutrients without considering all of the processes which contribute to its distribution. The proportions of phosphorus supplied by the various processes is of interest. The total assimilation during this period is calculated as 8.07 grams per square meter. Of this, only a little over 2% disappeared from the original inorganic phosphate in the surface water layer, 73% was brought to the surface by vertical transport, and, it is estimated on meager grounds, which, however, are the best available at present, almost 25% was supplied by decomposition within the surface layer. It is only by considering the entire picture, and the various

processes involved, that the whole story can be discerned.

Rather than close on too optimistic a picture of the problem, however, I would like to enumerate a few points concerning which our present information is altogether too meager.

(1) The knowledge of the composition of the natural populations of plankton is entirely too scanty to permit generalizations. The use of conversion factors which interrelate the various chemical, physical and biological properties of the populations will increase and be made more useful as the accuracy of the conversion factors improves.

(2) Direct evidence on the rate of decomposition of naturally occurring organic matter in the sea is greatly to be desired. If all of the other processes were known this could be inferred, of course, from the observations. The possibility of direct measurements in an isolated body of water should not, however, be overlooked.

(3) More accurate knowledge of the forces which control vertical mixing and transport of water are certainly desirable. This process, after all, accounted for 73% of the supply of phosphorus to the surface water in our observations, and it is the one factor most frequently neglected in studies of aquatic populations. The variations in the magnitude of these mixing processes with depth and stability of the water, with the seasons and the associated climatic changes, with wind and tidal currents must be more completely understood before the observed changes can be thoroughly explained.

When these additional pieces of the puzzle are available it will be possible to construct a balance sheet of the changes of any bio-labile element in the water with greater assurance than is possible at present.

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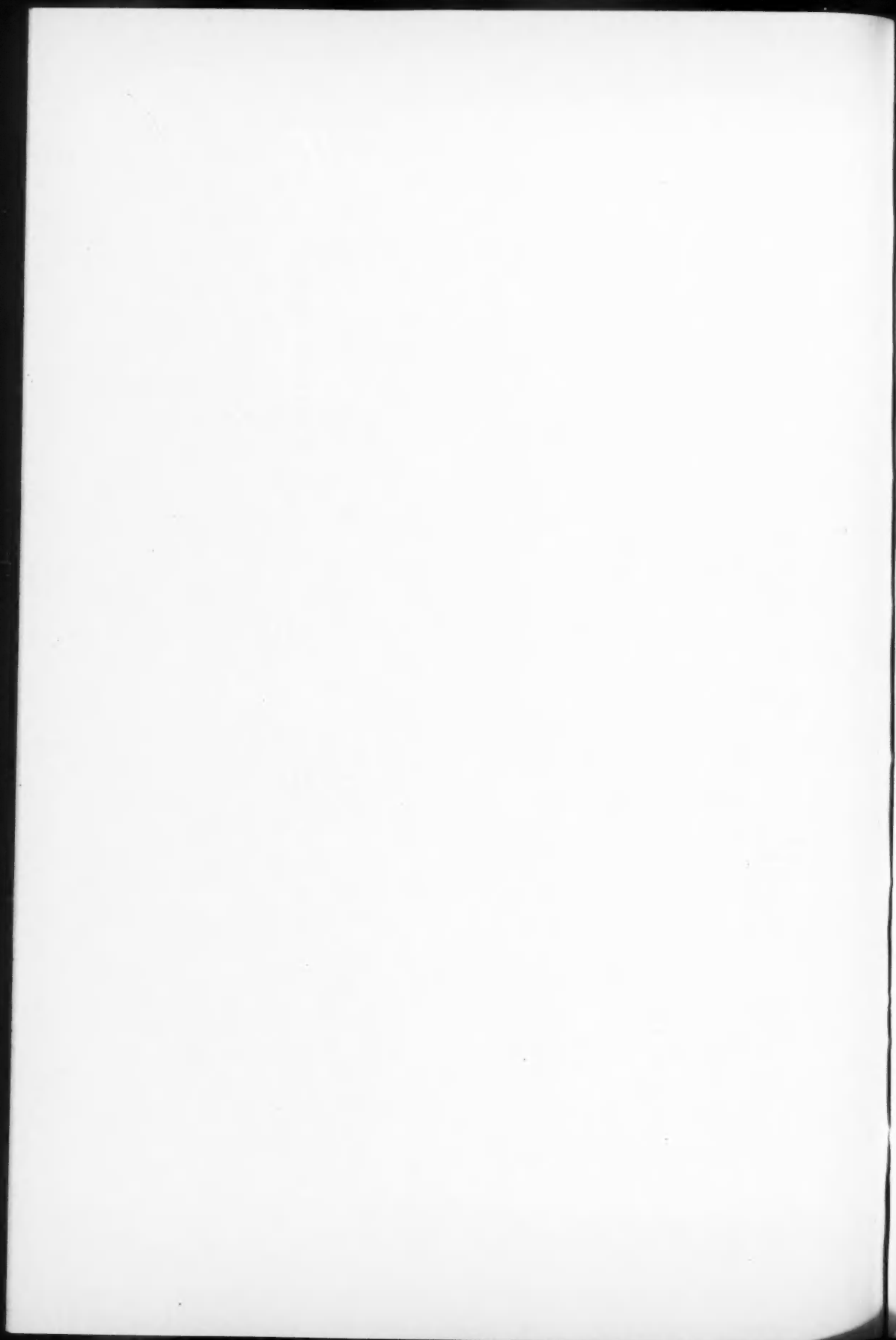
THE ROLE OF INTRASPECIFIC COMPETITION AND OTHER FACTORS IN DETERMINING THE POPULATION LEVEL OF A MAJOR MARINE SPECIES

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An understanding of the factors controlling the population level of marine fish is one of the most important objectives of marine biologists because of its bearing on the productivity of the sea in products useful to man, and, it might also be added, because we know so little about it. This paper will discuss some of the developments in a limited part of this field applying to haddock, one of the most important species of fish found off the New England Coast. Although this fish population is limited in comparison with the oceans as a whole, it is extensive in comparison with many terrestrial populations. In numbers it lies in the hundreds of millions; in extent it ranges over an area greater than the combined New England States without Maine and Vermont; while in observability it might be compared to a terrestrial population of comparable size shrouded in a dense fog when viewed from a dirigible cruising at a height of a few hundred feet (Fig. 1).

The first problem is to identify and evaluate the principal factors which control the population level of this species. Since it is impossible or impractical to control the environmental conditions, our procedure is to measure certain of the important environmental factors and compare their variations with variations in the population level.

Probably the greatest present limitation to progress in this field is the accuracy with which we can measure population size and population changes. If you question this statement, just consider how far beyond the speculative stage, knowledge of temperature, salinity, food supply, and other environmental factors will take you by itself. However, if you can obtain accurate data showing the changes in the population level which accompany variations in environmental conditions, you can begin to find out which factors are dominant and at what level they become important.

To measure population size, the most productive method now available to the biologist is to obtain records of fishing effort and catch, either commercial or sport, and from these calculate the returns per-unit-of-fishing-effort. This generally is considered as representative of the average density of the fish and proportional to the total population in the sampled area. Unfortunately, this is only approximately true,
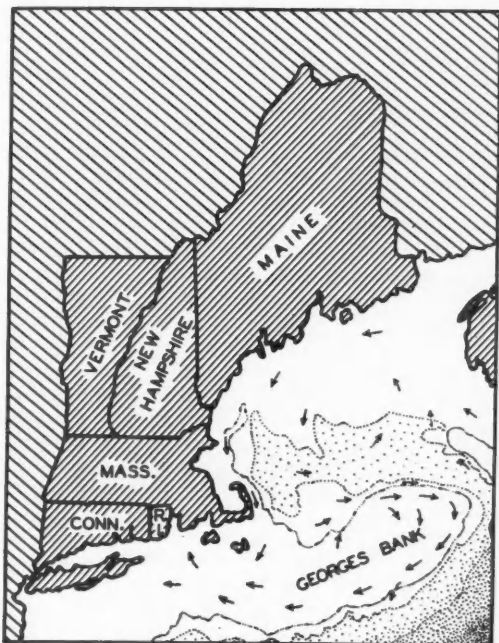
Fig. 1. Georges Bank in relation to New England. Arrows show the principal prevailing currents on Georges Bank and in the Gulf of Maine. The unshaded area represents the fishing grounds.

and technological changes in the fishery make it difficult to obtain comparable data on fishing effort, particularly over a long period of time. However, in spite of these limitations, statistics on catch and fishing effort provide the biologist with invaluable data for studying populations.

Studies of Georges Bank haddock provide a good example of some of the uses of these data. This species is preponderant among the larger fishes in the area, and a large amount of data have been accumulated bearing on fishing intensity, mortality resulting from the commercial catch, and other biological data. An index of the magnitude of the population of commercial-size fish has been calculated, in-

eluding adjustments to correct for all technological
changes the effect of which we have so far been able
to measure.   These include changes in the capacity
of the sampling mechanism (size and power of the
fishing boats), major improvements in gear, gear
competition, and adoption of technological improve-
ments such as wireless and sonic sounding.   How-
ever, we have not yet determined how closely the
final curve represents the actual population.   Nor
have we yet ascertained what bias the schooling habits
of the fish may exert upon our sampling apparatus
at different population levels (Fig. 2).

In spite of these limitations of the data it is pos-
sible to obtain a considerable amount of information
concerning population relationships from the popu-
lation index and other available data.   It has been
found in the Georges Bank area that usually the
greater proportion of the haddock between 1½ and
2½ pounds in weight (a market category called
"scrod") taken in the spring, are three-year-old fish.

The spring population index for these scrod, there-
fore, provides a rough measure of the relative re-
cruitment from the spawning which occurred three
years earlier.   Thus, by plotting the population index
for adult haddock (nearly all Georges Bank haddock
landed by the the trawlers are mature) against the
spring index value for scrod three years later, it is
possible to obtain a rough measure of the relation-
ship between the size of the spawning population and
the production and survival of young (recruitment)
(Fig. 3).

The decreased values of the recruitments at lower
spawning stock levels are reasonably explained as
resulting from the fewer eggs produced; but the
inverse relationship at high levels indicates that for
such stocks, factors other than abundance of eggs
dominate.   The most probable factor is competition
within the population.   Certain lines of evidence, in-
cluding the distribution of young and adult haddock
on the fishing grounds at different seasons, suggest
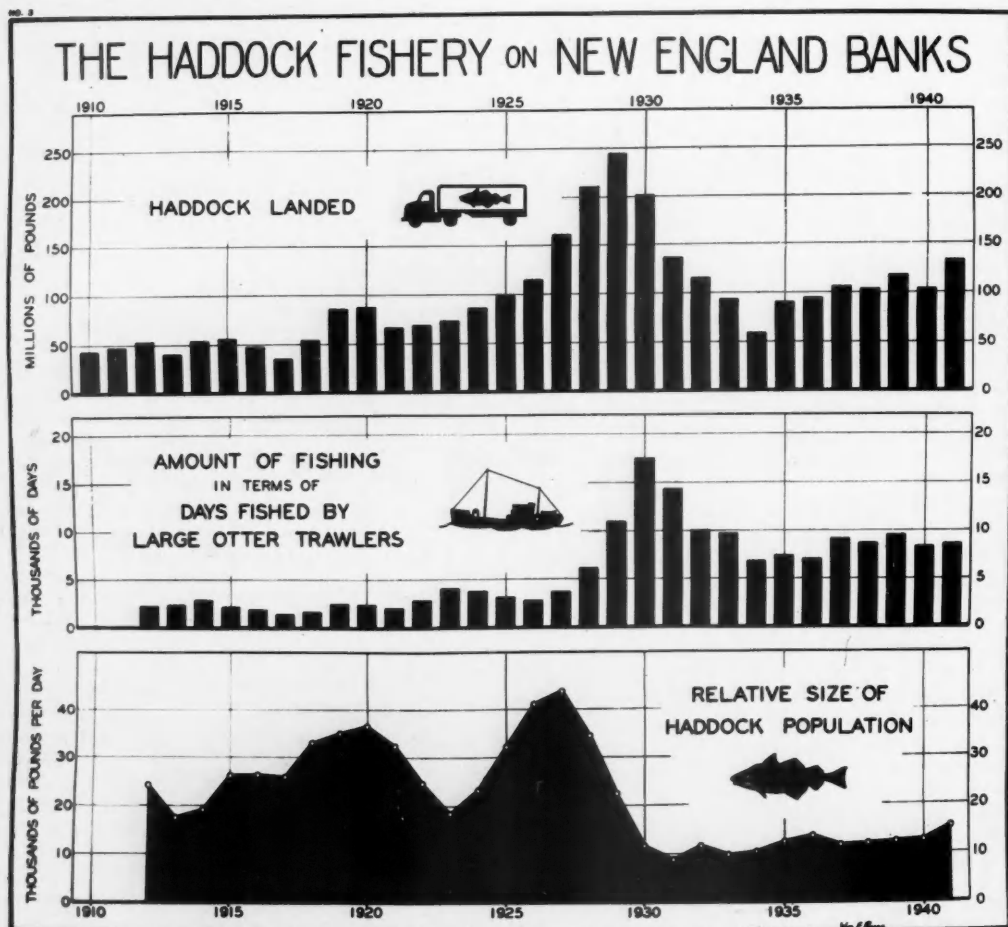
FIG. 2.   The haddock fishery on New England Banks.   The annual landings, fishing intensity, and variations
in the relative population level of commercial size haddock (Abundance index).
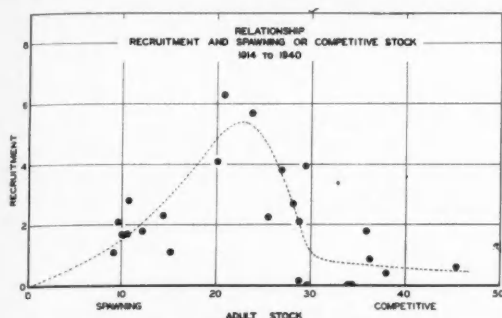
FIG. 3. Relationship between recruitment of young haddock to the commercial stock and the spawning or competitive stock, 1914-40. The dotted curve was fitted by eye to indicate the probable average relationship.

that this competition is most severe during the first winter when the young are about 10 months old. Therefore, the values for adult stock in Figure 3 are represented by spawning stock for the left-hand part of the chart and winter adult stock for the right-hand part.

The relationships shown in Figure 3 suggest that the overall factors controlling recruitment are spawning stock (number of eggs) at the lower population levels and adult stock (intraspecific competition) at the higher levels. The deviations from these dominant relationships result from errors in the population index and from other environmental factors which may cause unusually high or low mortality in individual years. Thus, they superimpose additional patterns of variation upon the basic relationship between recruitment and adult population.

These data for 1914-40 indicate that to maintain the maximum recruitment the spawning stock should be maintained at a level corresponding to a catch of 20-23 thousand pounds per day by large otter trawlers. Above that level increasing intraspecific competition overbalances increased egg production, while below that level decreasing egg production overbalances decreased competition. Thus, to achieve maximum recruitment, it is just as important to keep the competitive stock down as to keep the spawning stock up. This is a conclusion not generally acknowledged in marine fishery conservation, and I do not believe that the relationship has been demonstrated so clearly before. However, numerous parallels can be found in the case of domesticated animals.

We had reached this stage in 1941 in our analysis of factors controlling the Georges Bank haddock population. At that time, the population had recovered considerably from the low point reached in 1931, and it appeared that reduction in fishing mortality, resulting from the war and a reduced fishing fleet, might allow the spawning stock to increase to the optimum level indicated in Figure 3. The stage appeared to be set for the demonstration of our theory. That is what we expected, but this is what happened.

In 1942, 1943, and 1944, there was a further increase in the adult stock, as had been expected. However, by the summer of 1945 it became clear that recruitments from 1941, 1942, and 1943 spawning were very poor, instead of approaching the high levels anticipated. This reversal of the expected pattern has been the principal subject of our studies since work on this problem was resumed after interruption by the war.

The relationships between adult stock and recruitment since the expansion of fishing operations in 1929-31 are shown in Figure 4. This chart indicates a suppression of recruitment in the upper part of the adult population range, but at a level perhaps only one half as great as that found for earlier years (Fig. 3). The maximum recruitment occurred at an adult population level corresponding to a catch of 12-13 thousand pounds per day, instead of the 20-23 thousand pounds per day found in earlier years. Thus, although the adult stocks in 1941-43 approached the level which in earlier years resulted in very high recruitments, the production in recent years was very poor. The only previous years which produced such poor recruitments were those in 1925-28 and in 1917-20. In both cases, the adult stocks were about double those in 1941-43.
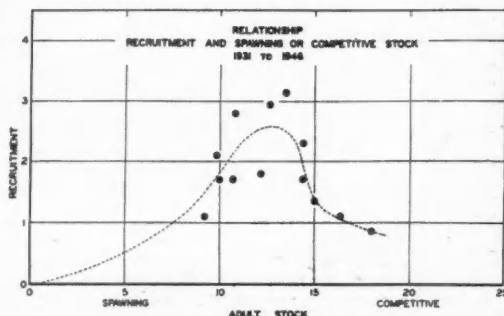

FIG. 4. Relationship between recruitment of young haddock to the commercial stock and the spawning or competitive stock, 1931-46. The dotted curve was fitted by eye to indicate probable average relationship.

In attempting to reconcile the relationships shown in Figure 3 and Figure 4, there appear to be two mutually exclusive lines of reasoning open to us.

The first is to the effect that the population index for recent years is not comparable to that for earlier years, but that, in fact, the population in 1941-43 was comparable in size to that during previous periods when recruitment was suppressed by intraspecific competition. Several lines of evidence and reasoning refute this explanation. The total catch of haddock from Georges Bank by all types of gear was about 211 million pounds in 1928 compared to an average annual catch of 117 million pounds in 1940-42. The now obsolete steam trawlers fishing in 1928 caught more haddock per day than did the modern Diesel trawlers using improved gear and greater power in 1940-42. If the populations in 1928 and 1940-42 were of comparable size, this could not have occurred.

Data on size and age of the haddock taken in 1928 and 1940-41 show that in 1928 the fish averaged nearly 3½ pounds in weight and between 5 and 6 years in age. In 1940-41 the catch averaged about 2½ pounds in weight and between 3 and 4 years in age (Fig. 5). Thus, in spite of the larger catches in 1925-28, there was a much higher rate of survival of commercial-size fish during those years than in 1940-42, which allowed the greater accumulation of older fish shown by the 1928 data. This again indicates that the population level in 1928 was much higher than that in recent years.

The second line of reasoning we have followed in seeking an explanation for the poor recruitments from the 1941-43 classes starts with the assumption, which is supported by the evidence just reviewed, that the population index represents the population level with reasonable accuracy. This leads to the conclusion that the poor survival from the 1941-43 year classes must have resulted from a change in conditions on the fishing grounds since the earlier years. The adult stock-recruitment relationship further suggests that the change has been such that the population level at which competition becomes dominant has been reduced to not much more than half of that which was found originally.

It is possible to theorize on many changes in the ocean which could have caused the poor survival of
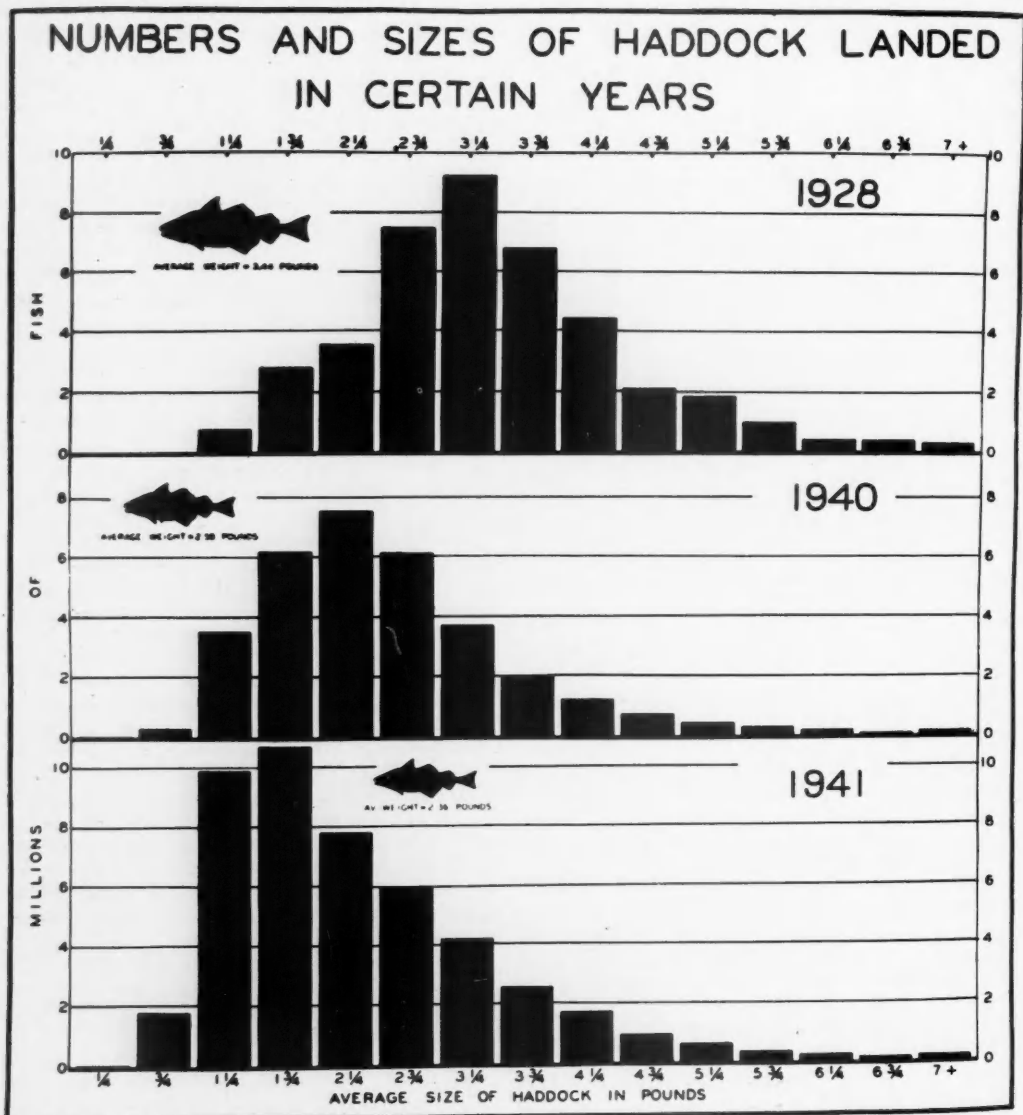
FIG. 5. Numbers and weights of haddock landed in 1928, 1940, and 1941.

young haddock of the 1941-43 year classes. Numerous examples of extreme variations in abundance of fish populations have been described in the literature. The North Atlantic mackerel and North Sea herring are outstanding examples. Little is known definitely about the causes of such variations although there has been much speculation. In the case of Georges Bank haddock, we have shown that poor recruitments, such as those from the 1941-43 year classes, have occurred previously. Moreover, a large mass of evidence has indicated that the poor recruitments in these earlier years resulted from poor survival of the young because of competition for food. No other abnormalities in the environment adequate to account for such a major change in mortality of young haddock have come to our attention during recent years. Consequently, food supply, which was the limiting factor in earlier years, appears to be the most promising factor to examine in seeking an explanation of the apparent reduction in the population level at which intraspecific competition became dominant.

Reduction in the supply of food available to the haddock population would most probably result from one of the following two developments:

1. An increase in the populations of competitive species would reduce the amount of food available to haddock. Records from the otter-trawl fishery show that on Georges Bank the landings of marketable species other than haddock have increased only about 4 thousand pounds per fishing day, making the average landings per fishing day of all species about 23 thousand pounds in 1940-42, compared to about 40 thousand pounds in 1928. This increase in "other" species probably reflects the improved marketability of these species more than an increase in their abundance. Less complete records on the abundance of species not saved for market, obtained from fishing trips in 1931-32 and 1940-41, suggest an increase between these years sufficient to raise the amount caught by otter trawlers by not more than 5 thousand pounds per day (Herrington, Wm. C., Rounsefell, G. A., & A. Perlmutter 1942). The increases indicated by these two lines of evidence are not sufficiently large to account for a major share of the apparent reduction in food supply for haddock, to perhaps one half the earlier level.

2. The alternate explanation for the reduction in the food supply is that the total amount of haddock food produced in the area has decreased greatly from the level existing in earlier years. What is the possibility that such a reduction could have occurred and what might be the cause?

To determine the possibility and identify the cause of a major reduction in the supply of haddock food, we must look for some condition, or conditions, which changed at the time the reduced supplies of food are indicated. I am aware of no natural events, such as change in ocean currents or temperatures, which might have caused such a major decrease in food production. However, there was a change in fishing operations and methods which might be related to the decrease.

Since the rapid expansion of the otter-trawl fleet in 1929-30, this form of gear has accounted for most of the haddock and other groundfish landed in New England, and the fishing intensity on Georges Bank has been high. The net used in this fishery is a large, flattened cone of netting with the sides extended as wings which are spread apart by large wood and iron otter boards or doors rigged to plane outward as the net is towed through the water. Prior to 1930-31 the lower lip of the net mouth was attached to a heavy wire footrope which had been wrapped with burlap and old rope to increase its effective diameter and prevent it from digging into the bottom. With this gear, fishing was confined to the mud, sand, and gravel bottom of Georges Bank, for rough bottom of rocks, barnacles, etc., cut the netting to pieces. In 1930-31, with the great decrease in the haddock population, increasing pressure was placed upon the captains and owners to improve the fishing boats' efficiency and expand the area of operations in order to hold their catches to profitable levels. Great wooden rollers 2 and 3 feet in diameter and 10 to 12 inches thick were strung on wire cables and attached to the footrope, and fishing operations were extended to rough areas never before fished. In the course of time, many of these areas were "improved" (?) by the heavy gear smoothing out barnacle- and shell-encrusted bottom, and by hauling rocks and boulders brought up in the nets to deep channels or gullies before dumping. Thus, much of the bottom previously classed as unfishable now is considered good fishing. Nearly all of Georges Bank can be fished regularly at present.

What effect have these changes exerted upon the food productivity of the bottom? The effect of otter trawling on the productivity of the fisheries has been the subject of investigation in England by two Royal Commissions and in the United States by the "Otter-Trawl Investigation" in 1915. No conclusive evidence on this subject was developed by any of these investigations. In a savings gear report in 1932 the author expressed himself as follows:

". . . The argument concerning the damage to fish food and habitat caused by dragging the trawls over the bottom has been confined largely to personal opinion as there is little definite evidence either way. We do know, however, that most of the small organisms such as brittlestars, mollusks, crustacea, etc., on which the groundfish feed, are sifted through the meshes of the net with little damage. . . . the evidence which is available on this question is largely indirect but in general indicates that the damage to the groundfish habitat and food supply is not momentous. . . ."

This statement about sums up the position of the otter-trawl controversy up to recent years. However, if the conclusions indicated by these recent population and recruitment studies on haddock are verified by further work, it will be necessary to revise considerably our ideas about man's effect on the productivity of the fishing grounds. Heretofore, it has been generally acknowledged by fishery biologists that the

catching of small fish and overfishing could affect
adversely the productivity of marine resources. This
work now suggests that under some conditions the
damage may be much more fundamental than that.
The establishment of this conclusion would be of
far-reaching significance, since this method of fishing
is one of the most efficient and wide-spread in use
today. However, because of the economic importance
of the method, its indicated harmful effect on bottom
food productivity must be established beyond any
reasonable doubt before this characteristic should be
used as a basis for conservation measures involving
any restrictions on the use of otter trawls.

At present, we have under way or in prospect sev-
eral lines of investigation designed to test the validity
of this theory. We have found that haddock growth
rates during the period of low population level in
1931 and later, were greater than those observed dur-
ing the immediately preceding period of high popu-
lation level. This indicates that the growth rate was
increased measurably by the greater amount of food
per fish resulting from the decreased population of
haddock. Studies are under way to determine the
growth rate of young haddock during 1941-43 for
comparison with growth during the period of high
population level in 1926-28 and low level in 1930-31.
If the growth in 1941-43 is comparable to that during
the years of high population level, it would indicate
that the amount of food per fish was about the same
during recent years as during the previous period
of much higher abundance. Since the population in
1941-43 was less than 50 percent of that in 1926-28,
and the considerable available data indicate that
there has been no increase in competing species suffi-
cient to compensate for the decrease in haddock, it
would follow that the total food available in 1941-43
had decreased about proportionately.

Unfortunately, this conclusion concerning decrease
in food cannot be checked by direct observation, since
no data are available for the earlier period. How-
ever, as soon as vessel facilities can be obtained it is
planned to secure measurements of bottom produc-
tivity for areas now fished, which once were listed
as unfishable, and compare them with areas still
rated in the latter category. It is also planned to
carry out experiments designed to measure directly
the effect of intensive otter trawling upon bottom
productivity.

The tentative conclusion concerning the effect of
otter trawling on bottom productivity brings up an-
other problem of importance to the aquatic biologist.
The decreased production of bottom organisms, indi-
cated by these studies, presumably was caused prin-
cipally by the reduction in surface area for a given
extent of bottom, resulting from intensive trawling
with heavy bottom gear. Such operations remove
rocks and boulders, and crush and level out clumps
of barnacles, shells, sponges, and other growths which
have accumulated over the centuries. Most of the
organisms upon which haddock feed are found on
or just under the bottom surface or attached to that
surface. Therefore, if it is assumed that the waters

flowing over the area contain adequate supplies of
food for these organisms, it follows that the total
supply of haddock food produced will be in some
measure proportional to the area of the surface ex-
posed to the passing water. If this is the case, then
what becomes of the increased plankton left in the
water by reduction in the number of bottom organ-
isms which feed upon it? Will there be an increase
in the pelagic organisms of the area which use the
same food? Will the adjacent areas over which the
water from the semi-denuded area next flows, produce
an increased crop of bottom organisms which in turn
will result in an increase in the populations of fish
found in these areas?

These hypotheses can be tested in two ways: First
of all, the actual quantitative production of fish can
be compiled for the successive sections or subareas of
the fishing grounds over which the water passes. If
the above-proposed hypotheses are true, then the de-
creased utilization since 1930-31 of water-born nu-
trients on the northern and eastern parts of Georges
Bank will have been balanced to a considerable extent
by an increased use of water-born food on Southwest
Georges and Southern New England grounds. This
should result in a corresponding increase in the fish
populations of these areas. Compilation of fish pro-
duction data, by subareas since 1928, now is under
way to determine whether such changes are indicated
by the commercial catch.

The second approach to this problem involves the
quantitative sampling of bottom organisms and water-
born nutrients over the various types of bottom for
the successive subareas. If a progressive decrease
in such nutrients is found along the path of the pre-
vailing current (Fig. 1), and the quantity of bottom
organisms on comparable types of bottom is in some
degree proportional to the quantity of nutrients, then
the validity of the hypothesis would be indicated.

These problems are of great importance to the
aquatic biologist and to all others concerned with
the productivity of the seas or other large water
bodies. If the tentative conclusions in respect to the
effect of otter trawling on the bottom are confirmed
by further study, they must affect the administration
of bottom fisheries throughout the world. Perhaps
the problem is to some extent comparable to that of
land erosion resulting from faulty methods of culti-
vation. The cure lies in determining how the gear
should be used in order to minimize its harmful ef-
fects, rather than in abolishing efficient producing
methods. The hypothesis concerning the relation be-
tween the degree of use of water-born food in one
area and the production of bottom organisms in areas
subsequently passed over by that same body of water,
also is of great interest. If true, it suggests that the
biologist, in drawing conclusions about certain types
and intensities of fishing, must consider not only the
effects on all of the species in a given area, but also
the effects on the populations in successive areas
along the path subsequently followed by that water
mass.

In this paper I have discussed some hypotheses

and theories concerning the factors controlling marine populations. Evaluation of such theories is one of the overall objectives of the aquatic biologist. However, the chief limitation on progress in this field today, is not so much theory or manipulation of data, as the ability to measure with a sufficient degree of accuracy the various factors which the biologist must consider. In view of the size of the populations with which we are working, the extent of the areas, and the difficulties involved in obtaining direct observations, it must be admitted that this is likely to remain a major problem. For that very reason it should receive increased attention and the biologist should make greater use of the assistance which physicists, chemists, engineers, and men of other professions can give him. Adequate financing of improved techniques also is essential if fishery biology is to continue its progress toward becoming a science instead of an art.

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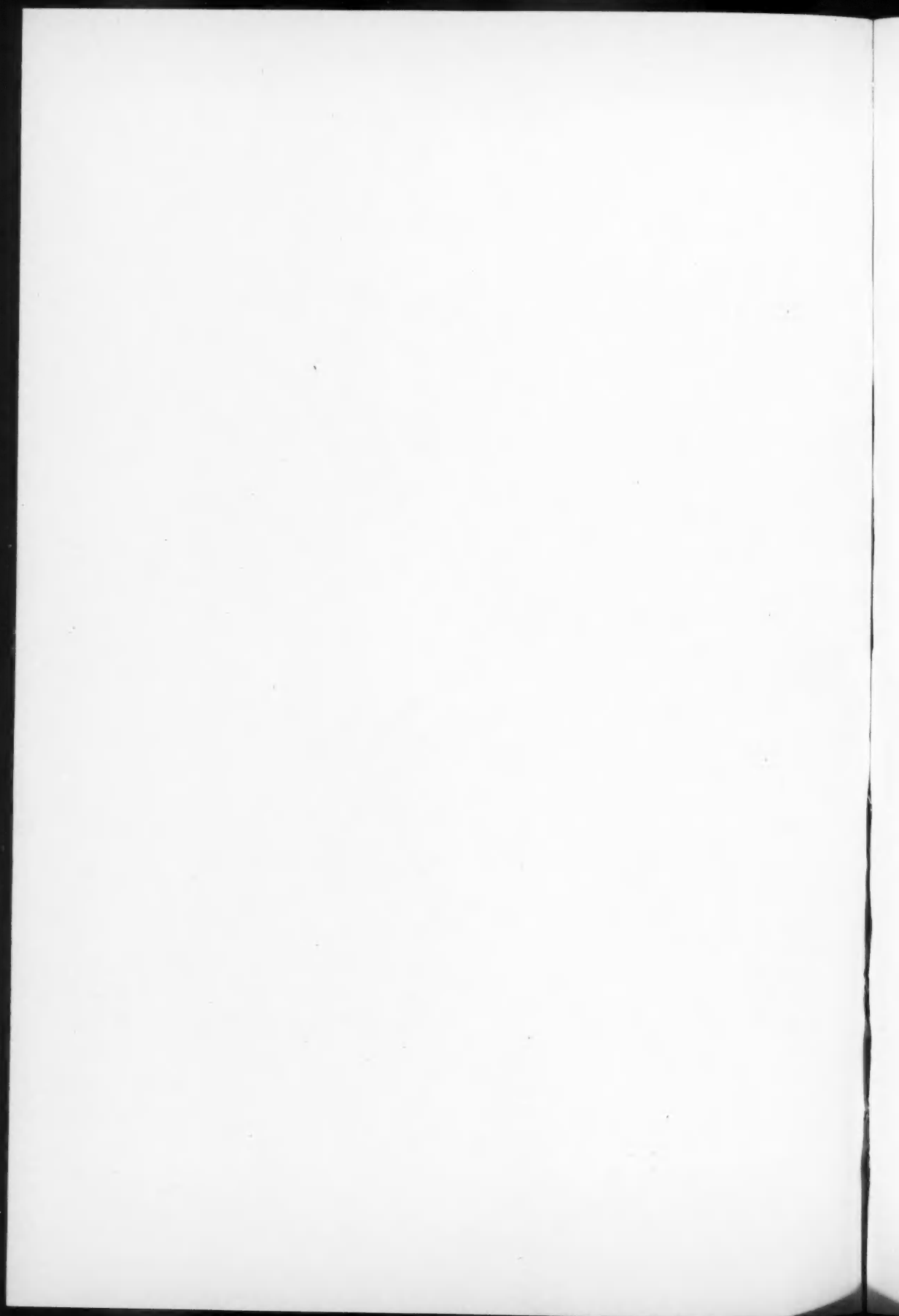
THE BASES FOR TEMPERATURE ZONATION
IN GEOGRAPHICAL DISTRIBUTION*

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INTRODUCTION

Zonation, as the term is employed here, refers to the limited north-south distributions which characterize most species. It is well known that these restricted distributions are to be interpreted largely or wholly in terms of temperature. In this contribution an attempt will be made to bring together the main points of our understanding of the relations between zonation and temperature, and to outline the system of logical generalizations which appear to follow from that knowledge. Attention will be confined to the fundamentals of the problem, leaving for a later discussion various matters of detail commonly encountered in particular cases.

I should like to express my appreciation to a number of friends and colleagues with whom this synthesis was discussed during its formative stages, and who contributed many helpful suggestions and comments. Particular thanks are due to Dr. A. C. Redfield, Dr. B. H. Ketchum, Dr. T. A. Stephenson, Professor J. E. Harris, Dr. E. S. Deevey, Jr., and Dr. I. M. Newell. Miss Grace Winter and Miss Margaret Scharff have assisted in the compilation of data, and Miss Scharff has prepared the maps and figures.

THE FUNDAMENTAL BACKGROUND

Investigation has indicated increasingly that zonal distribution boundaries must be correlated with winter or summer seasonal conditions. Dana (1890), Orton (1920), Appellöf (1912), Runnström (1929, 1936), Setchell (1893, 1915, 1917, 1920, 1920a, 1922), Schmidt (1909), and Parr (1933) are among those who have given particular impetus to such considerations in marine biology. Similar ideas have been developed, of course, regarding terrestrial forms, and the same sort of relationships to temperature apparently underlie the zonations of terrestrial and marine species alike. The concepts outlined below, therefore, are valid for either medium. Since this symposium is concerned with marine ecology, however, the discussion is confined to shallow water marine species.

The appreciation of the importance of seasonal temperatures in the control of distribution has emphasized two general types of relationship. In the first of these the dispersal of forms is checked where temperatures become too extreme for survival of the

individuals. In the case of a species spreading toward the poles an extreme temperature of this sort is encountered first as a winter temperature. The boundary comes into being where the species is subject to winter killing. For a species spreading toward the equator the comparable boundary arises where summer temperatures first become too high, and dispersal is checked by inability of the individuals to survive the excessive heat. The classic illustration of a marine distribution regulated in this general fashion is provided by the reef corals, apparently unable to survive where temperatures fall below about 70° F. at any time during the year, and accordingly confined within the tropics by poleward winter boundaries of this intensity. The interpretation seems to have been advanced first by Couthouy (1844), and was extended and popularized particularly by Dana (1890).

The second sort of relationship to temperature stressed in distributional studies involves the critical temperatures necessary for reproduction or completion of life cycles. In such cases species spread toward the poles as far as summer temperature conditions are adequate, and towards the equator as far as requisite low temperatures can be obtained in winter. A number of critical phenomena may lead to boundaries of this type, among them trigger temperatures necessary to induce spawning, and growing seasons of adequate duration as well as intensity. Frequently it appears that a critical temperature is directly concerned with the process of reproduction, as in the case of the sponges and oysters studied by Orton (1920) and others. Often, again, the critical temperature is apparently to be sought in a larval stage, or at metamorphosis in sessile attaching forms. Thorson (1946) has recently reviewed evidence of a number of such phenomena. Boundaries depending on adequacy of the growing season—i.e., summer toward the north—are fairly well known. Setchell's (1920) studies on *Ascophyllum nodosum* and other algae whose reproductive or fruiting periods shift into the winter in the southern parts of their ranges may be cited as marine examples showing a comparable importance of winter temperatures for equatorward boundaries.

The important conclusion to be drawn from all such investigations is that distributions may be limited both toward the poles and toward the equator by tolerances or requirements which can be referred either to summer or winter seasonal conditions

There is considerable force of logic to this view. Distributional boundaries are extremes, and it is reasonable to study them in terms of the coinciding extremes of environmental conditions. There is the further fact derived from culture work and other laboratory investigations that most organisms have a given range of temperature over which survival is possible, and within the survival limits a somewhat narrower range of conditions over which reproduction and repopulation can be completed. Four critical levels can be recognized in these relationships, and are readily identified with the seasonal boundary conditions as in the following scheme:

Minimum Temperature for Survival—Winter poleward boundary

Minimum Temperature for Repopulation—Summer poleward boundary

Maximum Temperature for Repopulation—Winter equatorward boundary

Maximum Temperature for Survival—Summer equatorward boundary

This scheme summarizes, in effect, the previous comments.

Obviously, for a given species a given boundary point—poleward or equatorward—must depend on only one of the two possibilities. In general the choice will be determined by which of the two critical temperature conditions occurs geographically nearer to the center of dispersal—i.e., the limiting tolerance which would first be exceeded by further spreading of the species. Survival of the individuals and repopulation are both necessary for sustained, permanent establishment. The choice will also be influenced by the actual range of temperatures separating the two possible critical intensities in the physiology of the organisms. Thus, many forms are able to survive temperatures down to freezing, but reproduce only under rather warm conditions. Poleward boundaries of such species are almost certain to be summer ones established by the reproductive requirements. On the other hand, species whose minimum survival tolerance and minimum temperature for reproduction are close to the same intensity are more apt to be limited by liability to winter killing of the adults.

THE FOUR TYPES OF ZONATION

On these grounds there appear to be four basic types of zonation which can be recognized, Figure 1. These types are defined in terms of the sorts of boundaries at their poleward and equatorward limits. The simplest type is that in which the extreme temperatures for survival of the individuals are critical both north and south. This involves a winter temperature toward the pole and a summer temperature toward the equator, and is designated as Type 1. Type 2 is the exact converse of Type 1, and covers distributions bounded at both ends by temperatures required for repopulation, i.e. summer temperatures toward the poles and winter temperatures toward the equator. Types 3 and 4 are combination types, one boundary in each case depending on survival tolerances, and the other on reproductive requirements.

Both boundaries in Type 3 are related to summer temperatures, and both boundaries in Type 4 to winter conditions.
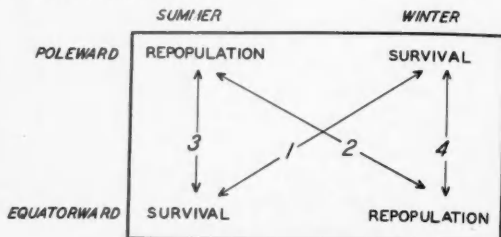

FIG. 1. Diagram of the four basic types of zonation, showing for each the season providing the critical poleward and equatorward conditions. The terms inside the box suggest the most usual sort of relationships involved —i.e. survival tolerance of the most resistant stage, or the requirements for some phase of the process of repopulation.

These four types are, in themselves, adequate for the interpretation of the distributions of many species. There are, however, more complex distribution patterns known whose analyses require inclusion of some further specific details of the life histories. Three such types may be noted briefly as illustrations of the point.

A common type is the seasonally extended distribution. Here, the species occupies a permanent range with at least one boundary of the survival sort. Given a motile stage, larva, or spore capable of dissemination by currents or winds, such a species may spread considerably beyond the survival boundary during the favorable off season, as toward the north in summer. Thus, many tropical forms appear more or less regularly during summer in Woods Hole waters, but are killed back again in the ensuing winters.

A somewhat comparable case may be found with a repopulation boundary involving the actual process of reproduction, as opposed to a larval tolerance. Beyond such a boundary a fringe population can be established which is maintained entirely by new infiltration from the permanent range. Under some circumstances the apparent outer boundary of the fringe area can be quite irrational as regards temperature, since it may be determined chiefly by the distance from the breeding stock over which dissemination is possible. Comparable distributions may result also from vegetative propagation beyond the breeding range, but presumably such processes more often lead to survival boundaries.

A third kind of variant distribution involves alternate mechanisms for the same boundary (poleward or equatorward), reproduction being critical on some coasts and survival on others. This is possible if the two physiological critical intensities are only moderately separated, due to the more extreme combinations of seasonal temperatures on some coasts as compared with others. Such a type of distribution is an inference based on the relationships to temperature accepted as conditioning boundaries. It is extremely

interesting, therefore, that seemingly good examples already have come to light. The best of these is for the barnacle *Balanus amphitrite*, which appears to have poleward limits alternately established by inability to survive winter monthly means of about 45° F., and inability to reproduce if summer monthly means do not attain about 65° F. On some coasts one, and on some coasts the other, serves as the limiting factor.

THE IMPORTANCE OF ZONAL TYPOLOGY

The importance of recognizing four basic types of zonation becomes apparent in considering the distribution of temperature. As already mentioned, the amplitude of the annual temperature curve varies from place to place. Summer and winter temperatures embrace much wider extremes in temperate latitudes than in the tropics or in polar waters, where relatively more constant temperatures prevail. In temperate latitudes, moreover, more extreme combinations of temperatures are found on the western shores of oceans than on the eastern ones. Along most of the North American Atlantic Coast, the annual range at any point is 25° F. or more, while in European surface waters the range seldom exceeds 15° F. A similar difference holds between the Asiatic and American Pacific coasts. It follows that points on two coasts

which have the same temperature at one season may have very different temperatures at the other season. Thus, in the Woods Hole region, the average maximum and minimum monthly mean surface water temperatures are around 68 and 38° F. The equivalent point on the European coast for summer temperature is about at Cape St. Vincent, Southern Portugal. The minimum (winter) monthly mean at Cape St. Vincent, however, is only about 58°, and to match the 38° found at Cape Cod, it is necessary to go well into northern Norway, to a point which in summer has a maximum monthly mean of only 50° F. Cape Cod thus is cotemperate with two points in Europe, one summer and one winter. These points, in turn, are cotemperate with other places on the American coast during the alternate seasons.

Because of such variations in the distribution of temperature, the four types of zonation result in geographically distinctive distributions of organisms. The four types, in fact, cannot lead to congruent patterns of occurrence, as is shown most simply by an example, Figure 2.

In Figure 2, maximum (summer) and minimum (winter) monthly mean temperatures at Newfoundland and at Cape Hatteras have been taken to limit distributions exemplifying the four types of zona-
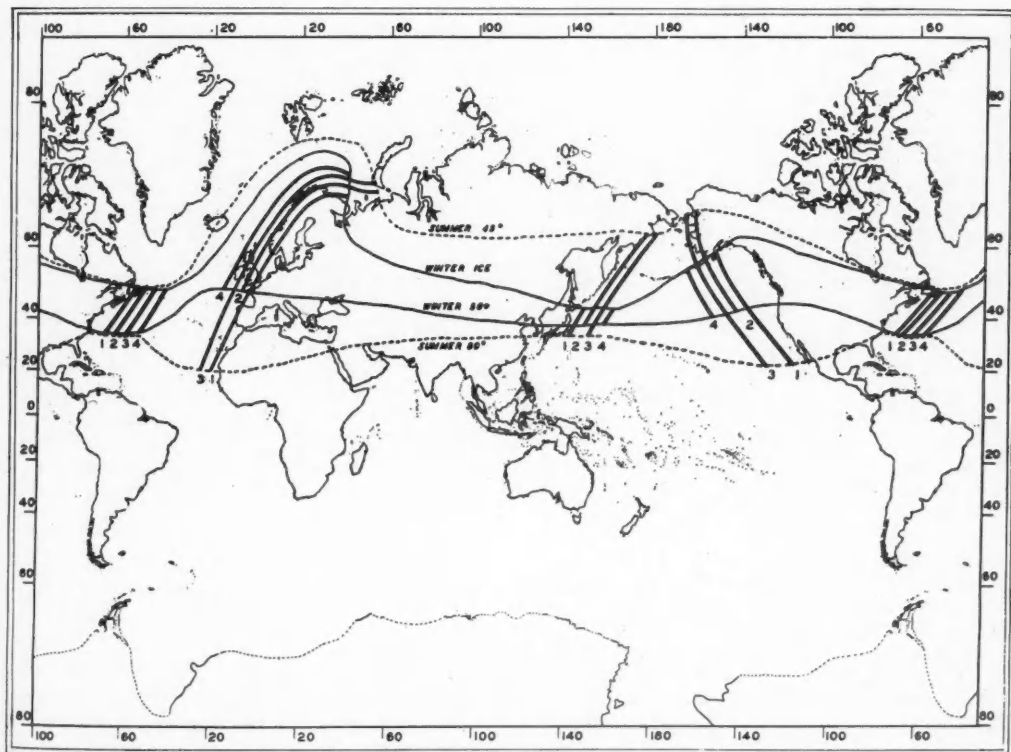
FIG. 2. Diagram showing the geographical extent on the major coasts of zones of the four types, using as limiting intensities monthly mean temperatures of surface water at Newfoundland and Cape Hatteras. The four types of zones are coextensive on the American Atlantic coast, but have independent, distinctive patterns of occurrence on other coasts.

tion. The respective values used are 45° and ice at Newfoundland, and 80° and 50° at Cape Hatteras. On the American Atlantic coast, the four types of zonation are thus given coextensive geographical ranges. The equivalent extent of each of the four types has then been determined for the other major coastlines, using the monthly mean temperature data from the Hydrographic Office "World Atlas of Sea Surface Temperatures" (1944). The isotherms in Figure 2, it may be noted, are schematic, and valid only for the major coastlines.

Since the four critical temperatures occur at separate places on each of the other coasts, there are considerable differences in the configuration of the zones of the four types. Four geographical ranges correspond on every other coast to the Newfoundland-Cape Hatteras range when defined by these temperatures, but no two of the four are coextensive on any other coast. It would thus be possible for four species, one belonging to each type, to have the same range on the American Atlantic coast, but entirely different latitudinal distributions elsewhere around the world.

Distributions conforming to these various sorts of patterns are common. For some species there is also evidence from physiological or other studies supporting interpretation of the distribution in terms of one or another zonal type and with particular limiting intensities. Two may be mentioned briefly, the common barnacle *Balanus balanoides* and the mussel *Mytilus edulis*. They appear to illustrate very closely, respectively, the type 2 and 3 zones of Figure 2, and because of this and certain other facts, the southern boundaries are of greatest interest.

The distribution of *Balanus balanoides* is indicated by some representative records plotted in Figure 3. The southernmost limits are at Cape Charles, Virginia (Richards 1930); the English Channel region (Moore & Kitching 1939); Akkeshi Bay (Hiro 1935); and Sitka (Henry 1942). The species seems not to have been reported authentically from Puget Sound, or the southerly Atlantic waters of America and Europe. This group of limits is better approximated by the minimum monthly mean of 45° F., as shown, than by the isotherm for any other monthly mean temperature.

The winter equatorward boundary implies that a low temperature required for repopulation is critical. It is striking, therefore, that while *B. balanoides* larvae settle and attach during the summer toward the north, as in Kola Fjord (Zenkewitsch 1935), fertilization occurs in late fall in the southerly parts of the species' range, as at the Isle of Man (Moore 1935), with attachment taking place in mid- or late
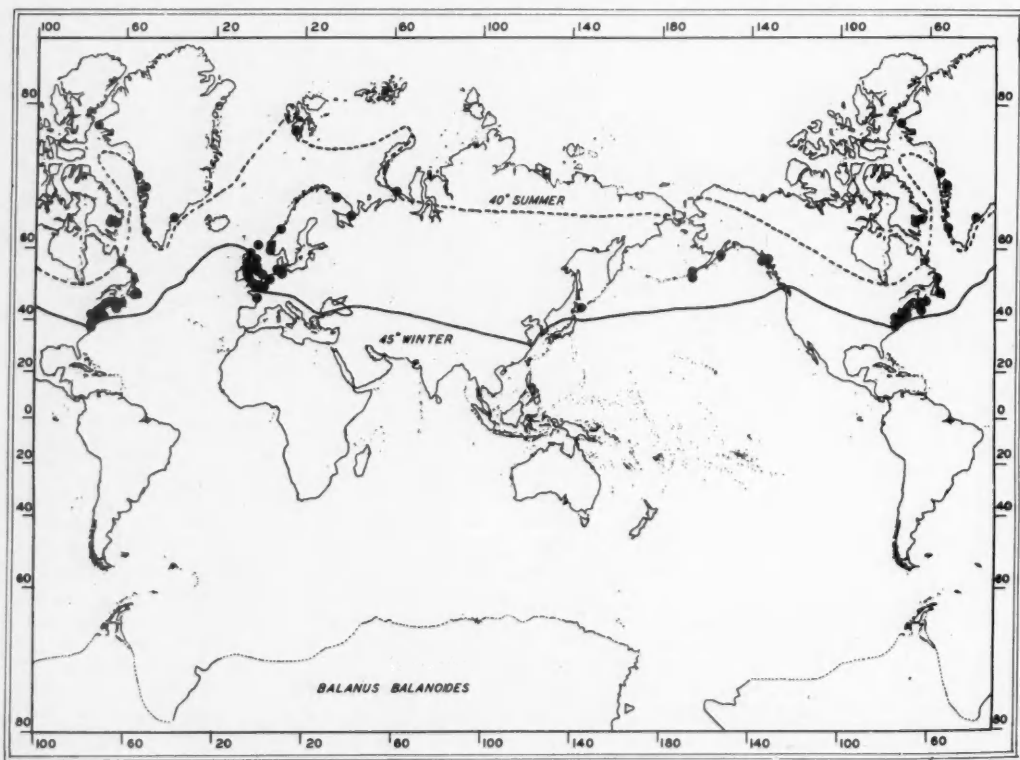

FIG. 3. Some records of the barnacle *Balanus balanoides*, showing particularly the apparent southern limits of the species. These limits are best fitted by the isotherm of the minimum monthly mean (winter) surface water temperature of 45° F.
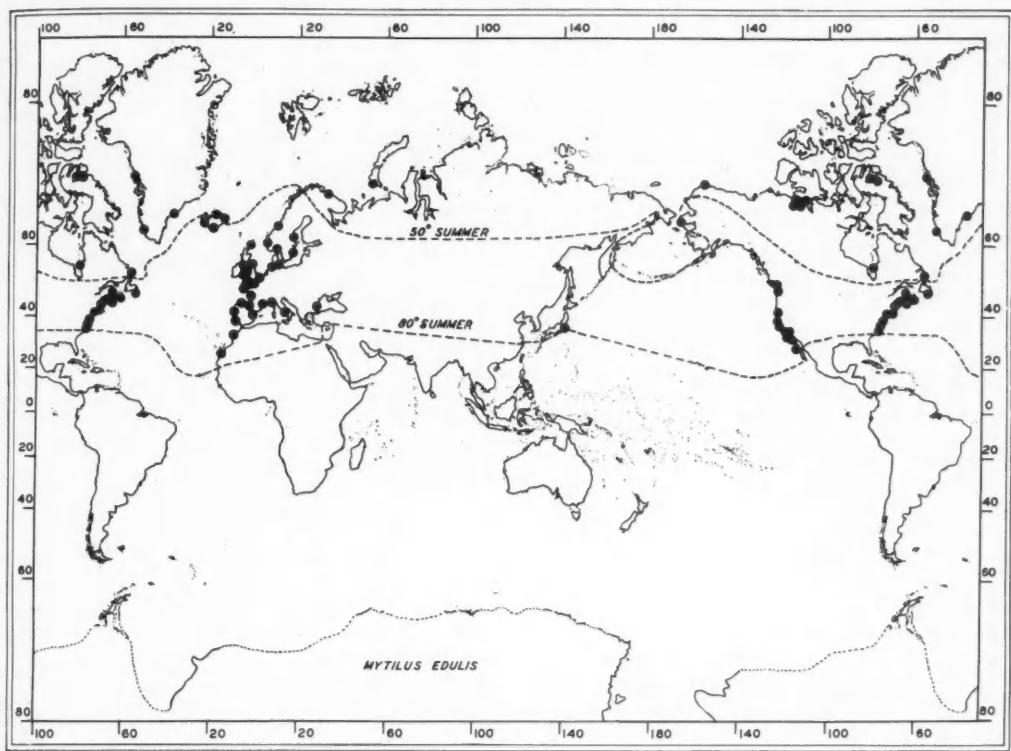
FIG. 4. Distribution of *Mytilus edulis*, with special reference to the southern limits. These are best fitted by the isotherm of the maximum monthly mean (summer) surface water temperature of 80° F.

winter. Winter is also the important season for re-population on the American Atlantic coast south of Cape Cod. Attachment in Long Island Sound occurs when water temperatures are at or near the minimum, in February or March. Larval stages are present at Woods Hole in the winter (Fish 1925), where attachment occurs in February, March or April. Attachment occurs at intermediate seasons in the middle portions of the species' range, as in June at Lamoine, Maine (Fuller 1946). Utilization of winter conditions to the south for repopulation is therefore clear. The interpretation derives final support from the note by Moore & Kitching (1939) that spawning is not accomplished by adults at the extreme limit of distribution in English waters.

Mytilus edulis (Fig. 4) has a similar extent on the American Atlantic coast, the most southerly records being from Beaufort, North Carolina (McDougall 1943, among others). The form is not common south of Chesapeake Bay.

The limit at Beaufort agrees quite exactly with what is known as to the maximum temperatures at which survival of adults of the species is possible. Ritchie (1927) determined by laboratory experiments that large mussels were killed in water of 84° F. after 14 hours' exposure, though they survived this temperature if transferred to colder water after a

4-hour exposure. Subsequently, it was found that mussels failed to grow in a conduit carrying sea-water periodically warmed to 83-90° F., though they grew profusely in a colder section. Bruce (1926) reported complete recovery after 1 hour at 86°, but indicated that longer exposures or slightly higher temperatures would be lethal. In view of these data, it is highly suggestive that even weekly mean water temperatures in Beaufort Harbor are about 83° F., with occasional maximum temperatures of 86-88° (McDougall 1943). Presumably the species is here at its greatest limit of tolerance, and the occurrence of slightly more extreme conditions to the south prevents its further dispersal in that direction.

The mussel's distribution on other coasts is less satisfactory for study, chiefly because the records for a number of varieties and even other species are confused with resultant uncertainties in the data (Lamy 1936). In the eastern Atlantic, however, typical living specimens of the authentic *edulis* have been collected at least as far south as Casablanca (Dr. C. J. Fish, private communication), and *Mytilus edulis* has twice been reported still farther south from Rio de Oro by Font y Saugé (1904). It is debated whether all the northern Mediterranean and Black Sea *edulis* records pertain to *galloprovincialis*, or whether both species occur in those areas as the records nominally indicate.

On the American Pacific coast, Dall (1921) and others have recorded *Mytilus edulis* from Bering Straits to Cedros Island, about half way down the outer side of the peninsula of Lower California. Over most of this range it is said to be common, though in the United States waters it appears to occur more often in bays and harbors than along the exposed outer coast. Some, and possibly all of the southern records, pertain to the recently recognized variety *diegensis* Coe (1946).

In Japanese waters, *Mytilus edulis* has a southern limit near Tokyo (Miyazaki 1938).

The various southern limits—West Africa, Lower California, and Tokyo—are consistent with that at Cape Hatteras, if the latter is interpreted as dependent on the maximum temperature which adults can survive. This is shown in Figure 4 by the course of the isotherm for the extreme summer limit of the monthly mean of 80° F. The southern boundaries of *Mytilus edulis*, in fact, are almost exactly those expected from Figure 2. It is obvious, of course, that the correlation with a monthly mean temperature involves a symbolic use of the latter; in general the 80° F. summer monthly mean is to be taken as indicating the occurrence of various combinations of conditions, partly suggested by preceding discussions, which actually are critical for *Mytilus edulis*.

The northern boundaries of both *Balanus balanoides* and *Mytilus edulis* can not be ascertained from present data. Most of the records plotted are from Madsen (1936) and Dall (1919). The more northerly of these records for both species refer to isolated, relict populations surviving in warm fjords or similar localities, and it is not possible to discover where the general ranges cease and occurrences of this type begin. Such outlying relict populations dependent on local summer warming which exceeds that for the general area, however, are in themselves characteristic of reproductive boundaries. Evidence too involved to present here, but based largely on times of attachment of the two species at a number of localities, suggests tentatively that the critical northern temperature for *Balanus balanoides* might be represented by the 40° monthly mean during the time of maximum temperatures, and that for *Mytilus edulis* by the similar monthly mean of 50°. These isotherms are shown on the maps, but are to be thought of only as probable first approximations of the northern limits of the general ranges of the two forms.

Figure 5 is a second map of the extent of zones of the four types, comparable to Figure 2, but based on temperatures obtaining in the western British Isles and at Cape Blanco in Africa. The limiting monthly mean values used at the north are 62° F. in summer
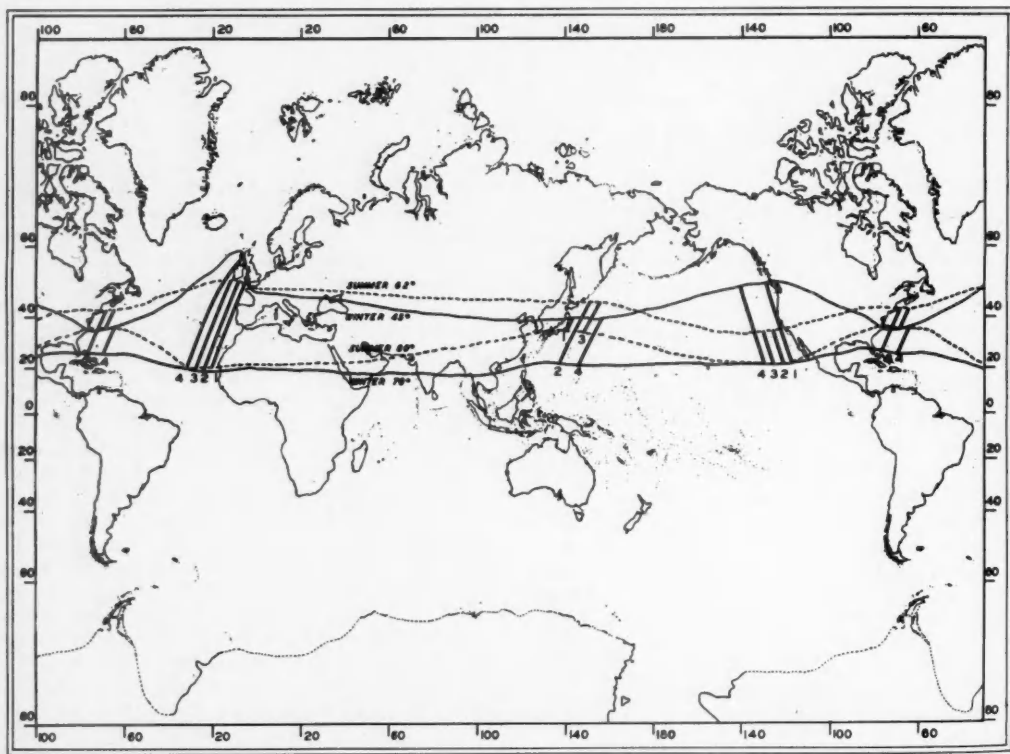

FIG. 5. Diagram of the geographical extent on the major coasts of zones of the four types, using as limiting intensities monthly mean surface water temperatures in the British Isles and West Africa. On the American Atlantic coast Type 1 is excluded, and 3 and 4 are segregated, by occurrence of the northern winter and southern summer limiting temperatures as the same point. Compare with Figure 2.

and 45° F. in winter, and at the south, 80° and 70° respectively. It is again shown that although the four zones are roughly coextensive on one coast, they are not on any of the others. The differences, however, are more extreme, due to the fact that the limiting northern winter temperature and the southern summer one occur at nearly the same point on the American Atlantic coast. As a result, the types 3 and 4, which are of parallel extent in Europe. are entirely separated in American Atlantic waters, and the type 1 zone, with these or narrower limits as regards actual critical intensities, can not occur at all. In Japanese waters the situation is comparable, though not quite as extreme as on the American Atlantic coast.

The Type 1 situation in this illustration is obviously a restatement of the familiar principle that the most steno-thermal European forms are excluded from the American Atlantic coast, owing to the great extremes of temperature obtaining throughout the waters of the latter. A species whose greatest survival tolerances embrace a range of not more than 25° F. can find no place to exist. Zonal typology, however, affords one possible explanation of the fact that only some species are so effected, out of a large number which might appear equivalent from their European distributions. Forms common to the European and American Pacific coasts, but undetected

by extensive studies on the American Atlantic coast, are especially open to interpretation as very stenothermal Type 1 species. The case of the hydroid *Syncoryne eximia*, shown in Figure 6, is an example. For these records I am obliged to Dr. E. S. Deevey, Jr.

INDEPENDENCE OF NORTH-SOUTH SYSTEMS OF ZONES OF THE FOUR TYPES

It appears, then, that four basic types of zonation need to be considered in studies of distribution. Each of these types must lead to the development of a complete system of zones over the world, utilizing the entire available temperature gradient with various combinations of limiting intensities. An indication of the implications of this conclusion can be obtained from a brief, simplified consideration of the American Atlantic coast.

On the Atlantic coast, important well-known biotic changes occur in the vicinity of Newfoundland, Cape Cod, Cape Hatteras, and along the Florida coast. Palm Beach may be taken here as the focal point for the latter. Using just these four change-points, fifteen components can be recognized in the whole biota from the Arctic to the Tropics, Figure 7. Fourteen have at least one termination along the coast—i.e., they are zonal—while the fifteenth is ubiquitous. This is the conventional, generalized picture arrived
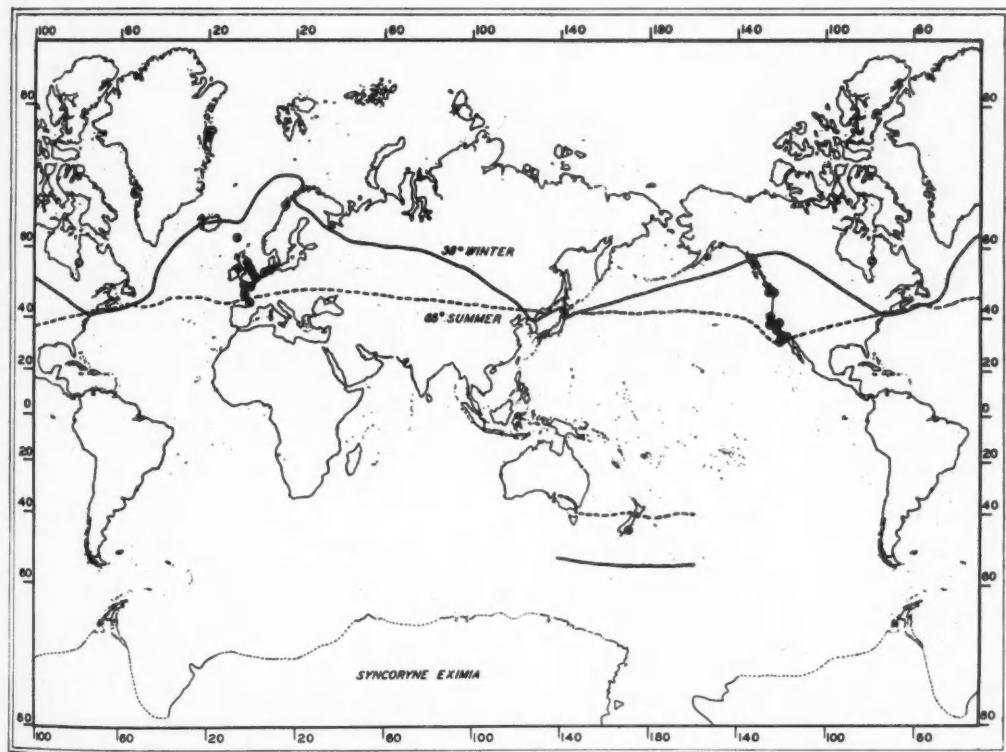

FIG. 6. Distribution records of the hydroid *Syncoryne eximia*. The main body of data agree with a Type 1 zonation as in Figure 5, with the limiting intensities indicated.
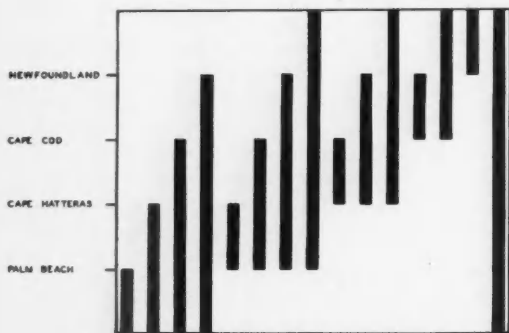
FIG. 7. Schematic representation of the components of the American Atlantic coast biota, with reference to the important change-points of Newfoundland, Cape Cod, Cape Hatteras, and Palm Beach. Fifteen possible ranges exist, of which fourteen are zonal and one is ubiquitous.

at by considering only the geographical ranges and describing them in terms of the four boundary localities.

The temperature data of the Hydrographic Office (1944), Parr (1933), and Fuglister (1947), show that at the times of maximum and minimum conditions, the isotherms are largely bunched at these same change-points, which thus are the locations of the temperature breaks (marked changes occurring in a short distance) with which biotic distributional data are correlated. On a scale of generalization comparable to that in the biological data above, these temperature breaks can be thought of as including all of the isotherms of the entire gradient occurring between Newfoundland and Florida. Neither gen-

eralization, of course, is strictly true, but they serve satisfactorily for present purposes.

The temperature breaks do not occur in both seasons at all the localities. At Cape Cod there is no break during the time of minimum (winter) temperatures, and in the Palm Beach area there is little or no thermal differentiation during summer. Newfoundland and Cape Hatteras, however, have breaks involving both maximum and minimum conditions. It may be assumed that at localities having a break at only one season, all the distributions terminating there are to be correlated with that break. If breaks occur in both seasons, then some of the distributional boundaries presumably are related to one season, and some to the other. It will further be assumed, here, that the sharpness of a biotic break is a direct reflection of the severity of the temperature break—i.e., the number of species affected in a given instance depends on the number of degrees of temperature change.

On this basis a provisional analysis of the Atlantic coast biota can be made in terms of zonal typology, showing the possible mechanisms underlying the geographical ranges of Figure 7. This has been done in Figure 8. Between Cape Cod and Palm Beach, each of which has a temperature break in only one season, only one type of zonation can exist (Type 2, limited by summer conditions to the north and winter to the south). For ranges bounded by either of these points and by a locality having breaks in two seasons, two zonal types are possible. Between Cape Hatteras and Newfoundland, each with breaks in both seasons, all four zonal types may be found.

In Figure 8, ranges which extend into the Arctic and Tropics have been handled as follows. Water of essentially uniform coldness is found in the Arctic
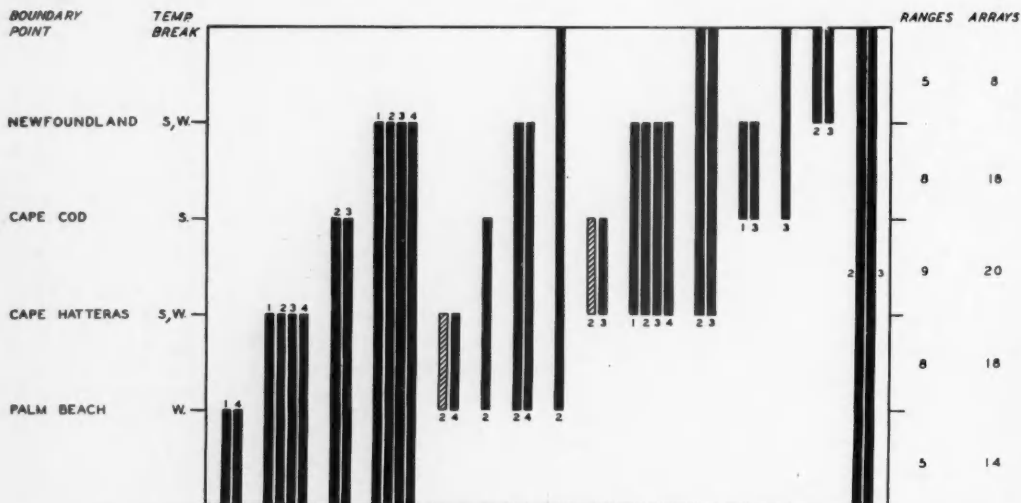

FIG. 8. Analysis of the biotic components in Figure 7 by zonal types. The summer and winter temperature breaks at the four change-points are indicated by initials. A separate bar (array) has been drawn for each zonal type contributing to each geographical range. The small figures show the type of each array. The figures at the right show the number of ranges and arrays contributing species to each province between breaks. For further explanation see text.

under the winter ice, and it is therefore taken as improbable that any poleward boundary north of the winter ice line (Newfoundland) is referrable to winter conditions. Summer alone is critical in the Arctic. This view, of course, is valid only for aquatic species. As for forms extending through the tropics, these exhibit no equatorward boundary, the southern hemisphere limit being a mirror image of that in the north. For theoretical treatments it must be assumed that some of these species have potential equatorward boundaries related to each season. In other words, if the entire annual temperature curve in the tropics were raised until the tropics became completely uninhabitable, some of the equatorward boundaries that would eventuate in the process would be conditioned by the new winter temperatures, and some by the new summer ones. This is the general analytical procedure that must be applied initially to any group of distributions extending *through* a center of warmth or coldness. Similar reasoning, it may be noted, has to be used in dealing with endemic species in places like the Gulf of Mexico or the Indian Ocean, where northern limits can be determined by geography rather than temperature, and true zonal boundaries may not be available for study.

The major general principle demonstrated by Figure 8 is that no zonal type contributes, at least in any significant measure, to all geographical ranges. By the way in which seasonal temperatures are distributed, each type is restricted to a definite pattern of possible north-south combinations based on actual intensities, and the pattern of possibilities is forced to be distinctive for each of the four types. The generalizations involved in grouping both the biological and temperature data for Figures 7 and 8 would allow, actually, for a few additional ranges and arrays—as a zonal type for a given range may be called—but these presumably would be exceptional cases without statistically important effects on the over-all conclusion.

At the right of Figure 8 the numbers of ranges and arrays contributing species to each biotic province are tabulated from the data in the figure. A province is taken as being bounded by any two consecutive boundary points, with a province also for the Arctic and one for the Tropics. The total number of ranges is 15, as noted in connection with Figure 7. Figure 8 shows 33 arrays altogether. It is interesting to note that the picture of distribution in terms of zonal types is very roughly about twice as complex as that in terms of ranges alone.

A point of passing interest is indicated in Figure 8 by the two Type 2 arrays with lined shading. Temperature conditions along the coast are such that in each of these arrays, a single monthly mean intensity is critical at both ends. The same temperature occurs at the northern end in summer that establishes the southern limit in winter. This implies that repopulation could not be carried out either above or below the single intensity, a situation which is obviously improbable as a proposal for any very large number of sessile marine forms. In effect, however, the situation is realized by migratory fish which follow an optimum temperature as it moves back and forth along the coast. Parr (1933) discusses the problem as it applies to the Cape Cod-Cape Hatteras stretch. This is another instance of the great variety of physiological relationships which can lead to a Type 2 zonation.

PROBLEMS OF COMPARING SEVERAL COASTS

The treatment of the Atlantic coast in Figures 7 and 8 is dependent on the existence of well marked breaks in the distribution both of the biota and temperatures, separating regions of relative homogeneity. The contrasts between the breaks and the homogeneous areas are sufficiently strong to lend value to the generalizations as approximate statements of the over-all picture. Similar treatments are possible for some other coastlines. There are coasts, however, which are much less easily divided into a few reasonably well defined provinces. Both the biotas and temperatures along such coasts change gradually, or at best have more numerous, comparatively small breaks none of which involve large numbers of species or isotherms. The European coast tends to be of the latter character, judging from the discussions by Ortmann (1896), Ekman (1935) and others. Ekman thus is notably careful to point out that an element of convenience, at least as much as any obvious natural facts, underlies his proposed boundary at the English Channel, separating his boreal North Sea region from the littoral of Southern Europe.

In dealing with coasts like the European, many more geographical ranges and arrays of distribution have to be recognized in order to attain a degree of truth comparable to that for the American coast in previous discussions. Since essentially the same total gradient of temperatures from maximum tropical heat to permanent polar ice is available on both sides of the Atlantic, for example, it follows that a number of arrays of one zonal type in European waters must be equivalent to a single array on the American side. The winter break in Florida includes monthly mean temperatures from about 55° to nearly 75° F.; in the eastern Atlantic, these same minimum winter temperatures are distributed from northern Spain to somewhat south of Dakar. Species common to the two coasts and bounded by such temperatures can differ considerably in European-African distributions, depending on their individual critical intensities within this 20° range, though all will share roughly the same boundary point on the American coast. Even in biogeographic comparisons of coasts with equally well marked breaks, similar difficulties must arise unless the temperature breaks on both comprise identical intensities, which is seldom the case for even one pair of breaks.

It is evident from such considerations that no very satisfactory map or other representation can be developed showing zonal distributions throughout the world at large. Each coast is sufficiently unique so that generalized intercomparisons have to sacrifice

practically all fidelity to detail, vitiating their interest and usefulness.

Although somewhat more bluntly stated, this conclusion does not differ in tenor from those reached or implied by many previous workers. Zonal typology, by showing how intricate the possibilities are for the merging, separation, and recombinations of distributions of organisms, provides a general formal basis for appreciating the truth of such views.

It is of interest in this connection to note how closely zonal typology has been approached by marine biogeography. Most investigators agree in recognition of a strong, well defined tropical zone. Commonly the boundaries of this are established where winter temperatures first drop significantly and conditions of relatively constant warmth no longer prevail. Ortmann (1896) used almost these words, for instance. In the high arctic, likewise, emphasis has been placed on seasonal conditions in interpreting the occurrences of organisms. The first departures from relatively uniform coldness throughout the year are caused by summer warm-ups of surface water, the importance of which is shown among other ways by the limitation of some arctic forms to cold, deep waters in southerly parts of their ranges. It seems to be only the failure to carry these principles of seasonal boundaries to logical conclusions respecting the temperate zones that has prevented an earlier statement of the thesis of the present contribution. It is remarkable that study of the American Atlantic coast did not lead to such conclusions long ago; the summer Cape Cod temperature break and the winter Florida one, each of which coincides with poleward and equatorward boundaries for many species, together predicate the whole argument.

The most extraordinary conclusions in this respect were reached by Setchell (1915 *et seq.*), whose ideas were very similar to ones still current in much terrestrial work. Setchell proposed to recognize a series of zones bounded by summer temperatures. These zones he then demarcated into subzones on the basis of the winter temperatures within them. Clearly this view incorporates all the fundamentals necessary to the present suggestion of multiple types of zones defined by their seasonal boundary relationships.

The difference of Setchell's conclusion from the hypothesis of multiple zonal types appears to have been conditioned by a preconception common in biogeography, namely that the world should be divisible into *one* series of geographically contiguous belts that will represent the main features of biological distribution. Probably this is a direct heritage from the historical background of regional faunistics and floristics, reinforced by the natural inclinations of the mapmaker and descriptive geographer. Granted a predisposition of this sort, proposals such as Setchell's are unavoidable consequents. It is inconsistent, however, to expect a single system of zonation to summarize even the empirical diversity of biological distributions, and certainly such a system is inappropriate as an interpretive summary for distributions

differing in kind because of distinctive causes of limitation. Since both maximum and minimum temperature conditions need to be considered, and since there is no rigid parallelism in the occurrence of the two, temperature itself can not be treated in biogeographical analysis as if it had but one variable, and a single series of temperature-controlled zones is impossible. It need hardly be added that any attempt to circumvent this fact by use of annual mean temperatures or similar methods is invalid.

APPLICATIONS OF ZONAL TYPOLOGY

The analysis of distribution by zonal types lends itself to a number of applications. First, it may be noted that the procedure is applicable to other conditions than temperature. Any seasonally variable conditions of comparable biological importance can be dealt with in the same way. As one example, the distribution of organisms in estuaries as related to salinity undoubtedly involves various types of salinity zones analagous to those related to temperature.

So far as temperature is concerned, study of distributions in terms of zonal types can be of use in guiding transplant work with commercially valuable forms, in predicting biotas of unexplored regions, and in various similar ways.

The most interesting possibility, however, concerns the determination of prehistoric environmental conditions. By studying the fossil distributions of selected series of forms, it should be possible to map the distribution of maximum and minimum monthly mean temperatures for earlier oceans. From these, in turn, some approximation of annual temperature curves might be inferred, opening up many avenues of inquiry for a science of paleo-oceanography. Merely as one example, Dr. Hutchinson in his contribution to this symposium has discussed the belief that the arctic has been appreciably warmer in the past than at present. It would be of great interest to know whether that warming involved significant differences in both summer and winter temperatures, or whether the summers only were affected. In the latter case there have always been low tmperatures at least in winter, which might greatly simplify the problem of the evolution of the present arctic fauna by justifying the existence of ancestral stocks suitably adapted to cold. There are independent reasons, of course, for an assumption that summer temperatures were chiefly affected, but a study of the fossil record conceivably could provide factual evidence with data on the the actual intensities.

SUMMARY

The main points of this contribution can be summarized in three sets of conclusions:

1. Zonal boundaries of organisms are to be interpreted in terms of summer and winter temperatures.

2. Four basic types of zonation can be recognized, each having a distinctive combination of summer or winter boundaries for its poleward and equatorward limits.

3. Zones of the four types have distinctive configurations around the world, and independent patterns of north-south occurrence. These facts depend on differences in distribution of summer and winter temperatures.

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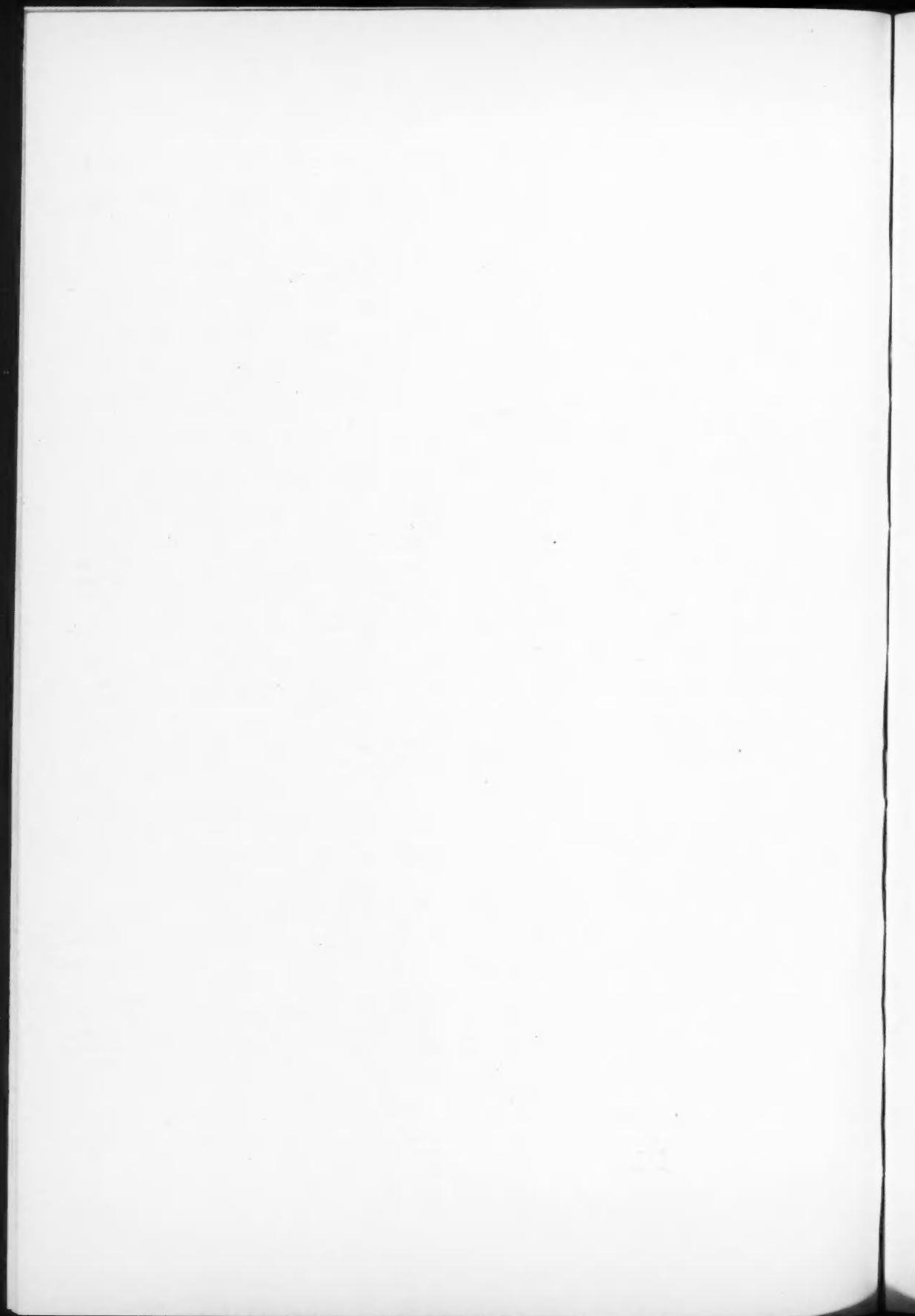
SOME CONTRIBUTIONS FROM THE LAND IN DETERMINING CONDITIONS OF LIFE IN THE SEA

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Dr. William Keith Brooks of the Johns Hopkins University over half a century ago in his monograph on "Salpa in its relation to the evolution of life" presents in the chapter entitled the "Discovery of the bottom and its effect on evolution" his reasons for belief in the origin of the bottom fauna of the sea from primitive pelagic ancestors. Taking this stimulating work as our point of departure let us descend through the clear depths of the sea, in which we have been floating for the past hour and a half, to spend a final few minutes in the mud of the bottom.

Interest in this zone received added stimulus this year with the appearance of ZoBell's most useful critical review, "Marine Microbiology," a book which every marine biologist and sanitarian should keep close at hand. From the wealth of material here presented it is evident that on and in the upper layers of the bottom occur chemical and biological processes as important to life in the sea as the various processes in the soil are to agriculture. Our concern this afternoon is the coastal zone within which photosynthesis can occur down to the bottom; the area over which river discharge exerts a measurable influence.

Physical Contributions

First to be considered are certain physical contributions from the land in determining conditions of life in coastal areas. The concentration of organisms at one narrow level on the surface of the bottom has lead, as Brooks points out, to fierce competition with consequent rapid evolution and adaptation in a multitude of ways. Nowhere else in the aquatic environment may such dense populations be found within such narrow vertical limits. We have taken more than 7200 Mactra lateralis, the dwarf surf clam 1.5—2 cm. long, per square meter, living in the uppermost 5 cm. of the bottom on the tidal flats of Cape May, New Jersey. Some animals, like the oyster, have fought it out at the surface, where through development of heavy shells they secured some measure of protection against their enemies. A fifteen-year-old oyster recently removed from Delaware Bay showed 87% of its total weight as shell; only 7% as soft parts. Other animals, notably worms and pelecypods, burrow into the bottom to varying depths where with lighter shells or tubes some measure of protection is afforded. Even here, however, a ceaseless struggle goes on; Natica, the predatory snail, penetrates into the bottom to destroy many Venus, Mya, and Solen, while from Delaware Bay southward giant sting rays

excavate deep pits with their wings, washing out hard and soft clams as well as other molluses for food. The rays, together with the chimaeras, and bottom feeding sharks, are typically bottom feeders with teeth adapted to crushing hard shelled molluses. Among these fish are some of the oldest of living vertebrates.

Of outstanding importance to all summer breeders is the heat brought into the coastal waters in river discharge and from water exposed over shallow flats at low tide. Water, thus warmed, carried by the late ebb or early flood tide over the bottom fauna may stimulate spawning at that time, whereas the temperature throughout the remainder of the tidal cycle may remain well below that necessary for reproduction. Setchell (1925) studying the temperature limits for growth and fructification of marine algae, of Zostera, and of land plants, assigned as critical temperatures for initiation of these processes 5, 10, 15, 20 and 25° C. Three years later we pointed out that marine pelecypods likewise show spawning temperatures closely associated, or identical, with these figures of Setchell.

There is some evidence that the disappearance of the oyster north of Cape Cod within historic times may have been due to overfishing the reefs on which these molluses were once abundant. Ingersoll (1881) estimates not less than eight million cubic feet of oyster shells in the kitchen middens left by the Indians at the mouth of the Damariscotta River, Maine. The ancient "fishweir" uncovered on Boylston Street, Boston, proves oysters to have been abundant here perhaps 4000 years ago (Johnson 1942). As the surface of the reefs was lowered the greater depth of water prevented the temperature within the oyster from reaching 20° C. for a period sufficient to initiate spawning. Orton (1920) placed the oyster among those marine animals which breed at a definite temperature which is constant for the species throughout its range. For Ostrea edulis, the European oyster, the critical temperature is 15° C. The American oyster, Gryphaea virginia, has for many years been supposed to require a minimum of 20° C. in order to breed, but recently Loosanoff (1939) has presented good evidence that spawning of oysters has occurred in Long Island sound at 16.4° C. or less, indicating possibly a critical temperature of 15° C. as in Ostrea edulis of Europe and in O. lurida of our own West Coast.

A substantial oyster industry exists in Prince Edward's Island, Canada, but although this marks the extreme northern limit of the oyster along the Atlantic seaboard, minimum summer temperatures over the shoal water oyster grounds here usually exceed those in the deep water oyster beds of Long Island Sound. From Delaware Bay south, however, our observations and those of others indicate that the critical temperature for spawning in the oyster has advanced from 20 to 25° C., putting the oyster into the same temperature group as the quahaug Venus. We may, therefore, have three physiological varieties within the species virginica, and it is of interest that more than a century ago Lamarck recognized from shell characters alone three species of oysters from our Atlantic Coast, with ranges approximately those just indicated.

Brooks emphasizes the destructiveness to pelagic life of the sediment in waters close to shore, and the intolerance to turbidity shown by corals, other than the genus Astrangia of temperate seas, is well known. Here and there among pelagic animals, however, are some possessing remarkable ability to cope with waters loaded with sediment. Among these is the ctenophore Mnemiopsis with its relative Beroe not far behind. The former has been found in Delaware Bay in great abundance with turbidities causing the disappearance of a Secchi disc in 0.1 meter or less (Nelson 1925). Its survival under such circumstances results from its ability to secrete copious quantities of thick mucus for long periods of time. Sagitta, a typical pelagic animal occurs in inland coastal waters of New Jersey which are very turbid. In April, 1919, two active speciments of Clione were found in a muddy tidal creek entering Great Bay, New Jersey. This pteropod is normally pelagic in clear ocean waters.

Some plankton feeding animals of our coastal waters have evolved elaborate mechanisms for the separation of their food from inert matter. Time will not permit discussion of this interesting subject further than to point out that at least in pelecypods, which have been the most studied, two morphological adjustments to high turbidity are found. Either the entire catch of food and mud collected by the gills is swallowed and sent to a food sorting caecum for separation as in the mussel Modiolus (Kellogg 1915; Nelson 1918, 1938), or separation to varying degrees of effectiveness occurs upon the gills and palps. The most effective sorting occurs in those forms like the oyster which possess a highly folded or plicated gill. The problem is here dismissed with the observation that some of the finest oysters with highest glycogen content in America occur on the one hand in Gardiner's Bay, Long Island where waters approach distilled water in clearness, and on the other hand along the Cape May shores of Delaware Bay in water so muddy that a Secchi disc disappears in less than 10 cm.

At the mussel purification station in Conway, North Wales, muddy grossly polluted water from the Conway River is pumped in upon the mussels in the purification basin. In less than two hours, even at temperatures as low as 1.5° C., Dodgson (1930) has shown that the mussels will transform 750,000 gallons of muddy water to limpid clearness, with more than 99% of the bacteria entangled in mucus lying on the bottom. Evidence indicates that muddy water may actually be pumped more rapidly by Mytilus than is clear water, due possbily to the phenomenon known as "anomalous viscosity."

Recent researches of marine bacteriologists, notably of Waksman, of ZoBell and their coworkers, confirm the observations of Drew (1912) off Andros Island in the West Indes, and place turbidity in a new light (ZoBell 1946). Each inert particle presents a surface upon which nutrients in solution are absorbed. Each such particle becomes a lodging point for great numbers of marine or fresh-water bacteria, with the result that water taken just above the bottom or on the surface of the bottom itself may show up to many thousand times more bacteria than the water a short distance above. Drew for example found at 800 meters depth off Andros Island 0 to 2 bacteria per ml. but 160,000,000 bacteria per ml. in the bottom itself. The importance of many of these bacteria carried down to the bottom by sediment in transforming organic matter into substances available to diatoms and other algae is just beginning to be recognized.

BIOLOGICAL CONTRIBUTIONS

This leads us to the second phase of our subject; the biological contributions from the land. We shall confine our attention chiefly to but a single species, the eel grass Zostera marina. Nature here has furnished us with a nicely controlled experiment by eliminating this plant over the Atlantic coastlines of Europe and North America during the early nineteen-thirties, Ostenfeld, 1908, Renn, 1936. In the two decades preceding its disappearance the Danes, notably Peterson and Blegvad, built up the theory that Zostera was the ultimate source of marine nutriment. Following its death in autumn the leaves disintegrated to form detritus which was considered to be the major food supply of all bottom animals. It was held that even plankton was of no use to the European oyster, Ostrea edulis, until it died and became a part of the detritus. No experiments were performed to determine the ability of the oyster to digest pentosans, but the importance of detritus to this mollusc was assumed solely from the fact that cattle are able to make use of this form of carbohydrate. Had the Danes followed this dangerous line of reasoning still farther to determine the role of bacteria in pentosan reduction in the cow they might still have made an important contribution to marine biology.

The experiments of Yonge (1926), however, proved conclusively that the European oyster is quite incapable of digesting pentosans, and within the next seven years Zostera itself disappeared from Danish waters. The oysters should promptly have shown lack of food, but there are no reports to date that they have done so. It was my good fortune to dredge
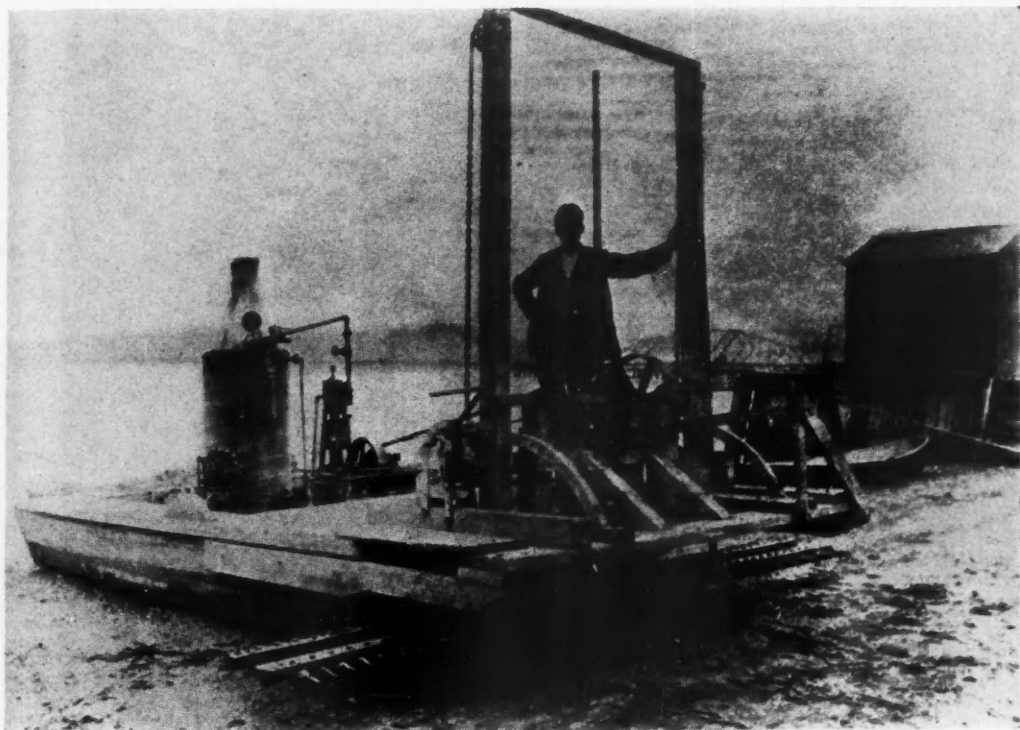
FIG. 1. Zostera mowing machine invented by Captain Charles T. Allen of Oceanic, New Jersey, in 1890, for removal of eel grass from his oyster beds in the Navesink or North Shrewsbury River. The capacity of this machine was 2500 square feet per minute. Mowing was done during the ebb tide, the current carrying the cut grass out to sea. This figure gives a graphic picture of the abundance of Zostera at that time. It is of interest that Peterson and Boysen Jensen, 1911, ignorant of Dr. Nelson's work, suggest, p. 76, the possibility in Danish waters of "improving the bottom-conditions by cutting down a portion of the superfluous vegetation by means of sailing or steaming reaping machines." They note that such machines have already been used to remove troublesome vegetation from European fresh waters. (From Julius Nelson, 1900, Report of the Biologist. New Jersey Agricultural Experiment Station for 1900: 359.)

in the Limfjord, North Jutland in company with Dr. Spärk of Copenhagen in 1931. From the great abundance of sea weeds present it was evident that ample supplies of cellulose were at hand to furnish whatever detritus might be required in the absence of Zostera.

Is it not possible, however, that the Danes were after all on the right track? Organic detritus contains vast numbers of bacteria. Wakesman et al. (1933) claim that 40% of the products of decomposition are incorporated into bacterial protoplasm itself. Because of their small size bacteria are readily engulfed by the circulating and fixed phagocytes which accomplish the bulk of digestion in pelecypod molluscs. The passage of detritus through the gut of a marine animal must thus yield a rich harvest of bacteria. With each return of undecomposed cellulose to the water after its passage through the gut it would soon acquire a new overgrowth of bacteria before being swept by currents into the food channels of another animal. Thus by repeated passages through the guts of detritus eaters fragments of

cellulose may eventually be transformed via the bacterial route into the protoplasm of marine animals incapable themselves of breaking down cellulose with their own enzymes.

In view of the error of the Danes in calling upon the cow for support of their theory of marine nutrition it is with some hesitation that I point to recent experiments which show that urea up to 5 pounds per hundred weight of food may be included in the diet of cattle and that this waste product is eventually turned, via bacterial protoplasm into beef. The possibility must never be overlooked that some marine organisms may harbor cellulose splitting bacteria within the confines of their own, often highly intricate, digestive tracts.

May I also utter here a word of caution: ingestion does not necessarily imply digestion, nor does the presence of living plankton forms in the faeces of any animal necessarily mean that such organisms are incapable of being digested. Failure to understand the mechanism for separation of food from sand and dirt in some pelecypods led Blegvad (1915) and
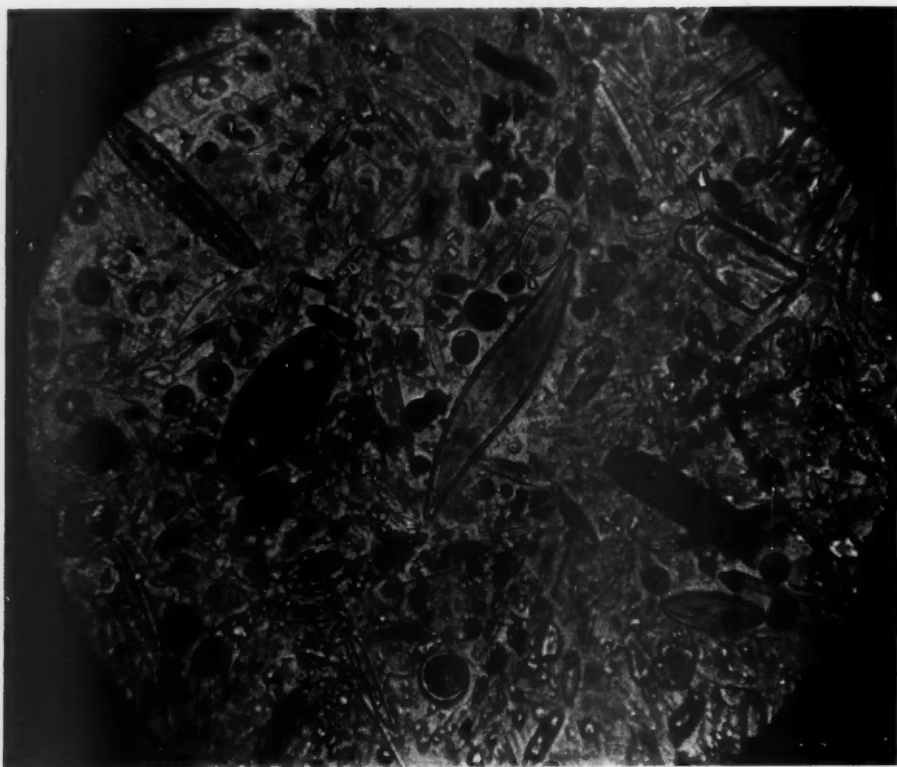
Fig. 2.   Stomach contents of oyster from Huey's Creek, Little Egg Harbor, New Jersey,
July 7, 1919.   This figure shows empty frustules of one large Pleurosigma, three Cocconeis, nu-
merous small Navicula and other genera.   A large diatom recently acquired shows oil globules at
either end and heavy chloroplasts as yet unchanged.   The abundance of empty frustules shown here
indicates that diatoms are digested by the oyster and at least the larger ones probably in the stomach.
(From Nelson, T. C., 1921.   Report Dept. Biology for 1920 Fig. 4, Reprinted pg. 109 in "Science
and the Land" N. J. Agr. Expt. Sta. 1941.)

certain others to totally erroneous conclusions re-
garding the availability of plankton organisms as
food.   In an animal which attempts any selection
while straining its food with the mud and sand from
surrounding waters, it follows that some intact
plankton will escape in the faeces along with the
inert matter.   This fact greatly complicates the prob-
lem of determining the food supply of economic
coastal species and of means of increasing this food.
Each species is a problem by itself, and may I admit
with complete candor and humility that even after a
half century of research on the oyster we are still
not in a position to say with certainty just what this
mollusc can or cannot use as food.   This is discour-
aging, especially in view of the statement of Dr.
Austin Clark twenty-six years ago that the oyster is
scientifically the best known marine animal in the
world.

Laboratory physiologists and marine ecologists
must combine their techniques; it is by no means as
simple as putting plugs of gelatin into an oyster's
stomach and concluding as did Yonge that the oyster

is a specialized herbivore incapable of extracellular
digestion of zooplankton.   Our own observations on
the American oyster reported in 1922 and 1933 and
extended by the researches of Dr. Mansour Bek in
1946 on the Egyptian oyster, species cucullata, east
doubts upon the validity of Yonge's conclusions when
applied to the genus as a whole.

CHEMICAL CONTRIBUTIONS

Third and last, the chemical contributions from
the land to the sea comprise the entire mineral con-
tent of the sea itself.   Some of the fundamental rela-
tionships between air, land and the oceans, have been
most ably dealt with by our first speaker this after-
noon.   May we limit our discussion to a few examples
of chemical elements which play special roles in the
life of coastal waters.

One of the most definite relationships reported
between a marine organism and a single ion is the
importance of copper in the attachment of the oyster.
Prytherch (1934) reports within a range of 0.05 to
0.6 mg copper per liter that the intensity of setting

of oyster larvae in Milford Harbor, Connecticut, is directly proportional to the amount of copper present. Subsequent metamorphosis of the larva into the spat did not occur in the absence of copper. Prytherch is able to induce setting of oyster larvae in the laboratory merely by placing a penny into a watch crystal of water containing oyster larvae, then removing it. He believes that the need for additional copper is correlated with increased amounts of this element entering into the formation of haemocyanin in the blood.

Attempts by others in America and in Holland to confirm Prytherch's observations have thus far been unsuccessful. This may mean only that in Milford Harbor the concentration of copper is such that it is the limiting factor at the time of attachment, whereas at the other locations it is not. Bearing upon the need for additional haemocyanin is the fact that upon and following attachment the oyster must depend upon the mantle alone for respiration until the gills develop and become vascularized. In Great South Bay, Long Island, in 1924 and in Barnegat Bay in 1925 the entire oyster set was killed in a few hours on the bottom where temporary low oxygen conditions prevailed. Only the spat attached to stakes and nets above the bottom survived.

Much has been accomplished in culturing diatoms in the laboratory, but do we know why, in nature, a certain species of diatom will thrive for a time almost to the exclusion of other species only to give way later on to another? What do we know regarding the relationships between diatoms and dinoflagellates? Are there specific substances carried down by rivers which stimulate the production of large numbers of certain species of diatom? What are the critical elements for the growth and reproduction of species of economic importance? Are some species of diatoms of more value as food than others, and may some forms like the spinous Chaetoceros and the long sharp ended Rhizosolenia be weeds of the sea indeed? Preliminary studies indicate that Chaetoceros is rejected to a very large degree by the oyster, while the non spinous *Skeletonema costatum* is eaten readily. Survey of the literature, however, reveals that we posses little data with which to answer the questions just given.

The program of the Limnological Society at these meetings with an entire day devoted to fertilization of aquatic areas, gives promise that some of these problems are well on their way toward ultimate solution. Gran (1931) showed that iron in sea water greatly stimulates the production of Skeletonema. Johnstone, working in Dr. Waksman's laboratory, has confirmed this using water from New Jersey oyster
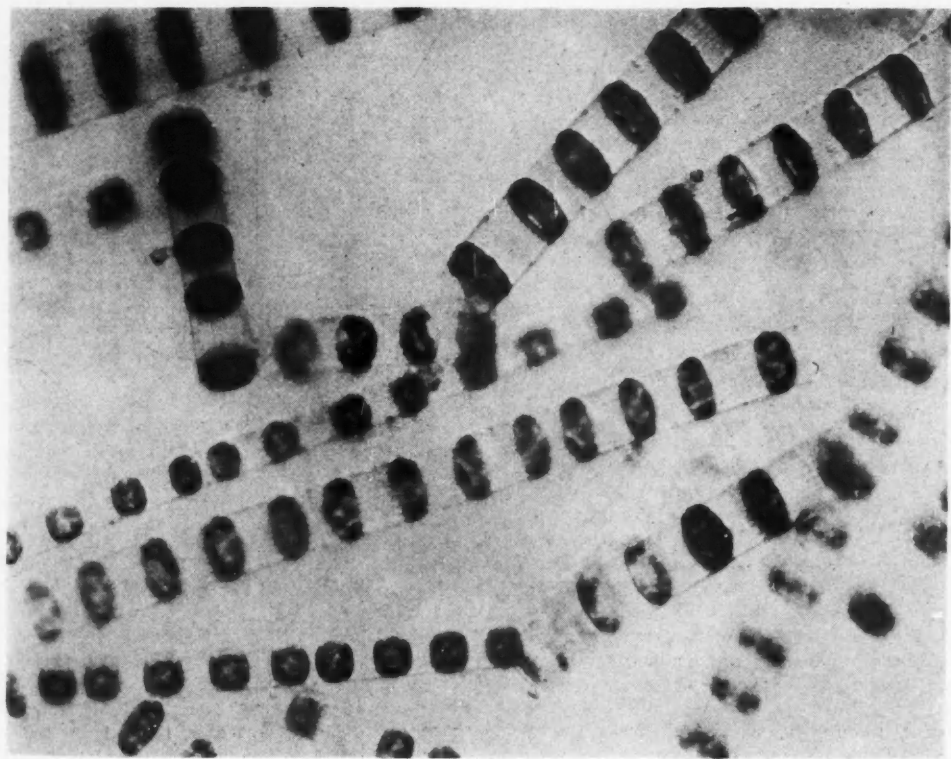

FIG. 3. Skeletonema costatum from plankton. This is the most valuable of all diatoms in the food of the oyster in New Jersey waters.
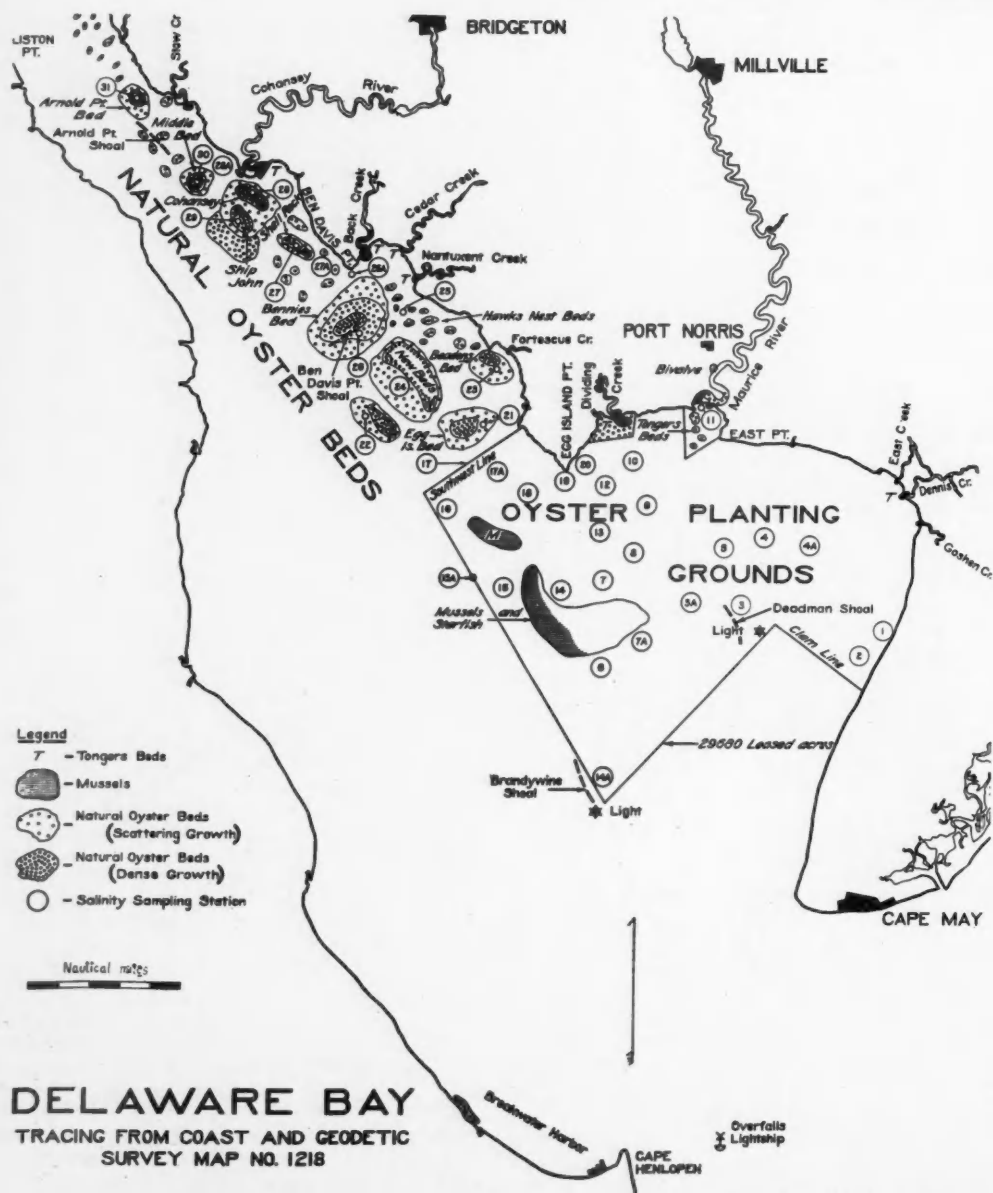
BRIDGETON

MILLVILLE

LISTON PT.

Arnold Pt. Bed
Arnold Pt. Shoal
Middle Bed

Snow Cr

Cohansey River

NATURAL OYSTER BEDS

BEN DAVIS

Back Creek

Cedar Creek

Ship John

Bennies Bed

Ben Davis Pt. Shoal

Egg Is. Bed

Nantuxent Creek

Hawks Nest Beds

Fortescue Cr.

PORT NORRIS

Bivalve

Maurice River

EGG ISLAND PT.

Dividing Creek

Tangers Beds

EAST PT.

Southwest Line

East Creek

Dennis Cr.

Goshen Cr.

OYSTER PLANTING GROUNDS

Mussels and Starfish

Deadman Shoal

Light

Clam Line

29680 Leased acres

Brandywine Shoal

Light

Legend
T   — Tongers Beds
   — Mussels
   — Natural Oyster Beds (Scattering Growth)
   — Natural Oyster Beds (Dense Growth)
○   — Salinity Sampling Station

Nautical miles

DELAWARE BAY
TRACING FROM COAST AND GEODETIC SURVEY MAP NO. 1218

Breakwater Harbor

CAPE HENLOPEN

Overfalls Lightship

CAPE MAY

FIG. 4. The natural oyster beds and oyster planting grounds on the New Jersey side of Delaware Bay. The Cape May flats referred to in this paper are located at 2 within the circle. (From T. C. Nelson, exhibits submitted with testimony, Delaware Diversion Case, U. S. Supreme Court, 1929. Reprinted in Perkins, E. B. 1931 "Story of an Oyster." N. J. State Bd. of Shellfisheries.)

beds. We reported in 1920 the great abundance of this diatom in Little Egg Harbor, New Jersey, reaching a maximum of 180,000 filaments per liter by the end of November. The diatoms made their appearance within two weeks after a hurricane August 13 which deposited 9½ inches of rain in 10 hours. In September, 1941, severe floods in southern New Jersey occurred during a cloudburst which reached a total of 13 inches in Atlantic City in 24 hours. Five dams burst on streams tributary to Delaware Bay resulting in heavy soil erosion. Again within two weeks Skeletonema appeared and persisted in large numbers for almost an entire year, during which the increased income from oysters harvested in Maurice River Cove was in excess of a quarter of a million dollars. Both in Little Egg Harbor and in Delaware

Bay the oysters were not only unusually plump due to high glycogen content, but their flavor was superior.

Skeletonema usually appears over the oyster beds of New Jersey and in Naragansett Bay during each winter, but in New Jersey at least it has only persisted through the warm months following heavy precipitation with attendant soil erosion. In view of Gran's observations, confirmed by Johnstone, is it not probable that organic iron liberated from the earth during extensive soil erosion was the factor stimulating this diatom? Lest anyone question the persistence of such an effect in Delaware Bay for a year the studies of Bigelow (1922) on the offshore coastal waters of New Jersey lead him to conclude that it takes approximately two years for the fresh water discharge of the Delaware River to escape ultimately beyond the tidal influence in and out of the Bay.

The observations of Dr. George L. Clarke (1940) are of interest in this connection. Zooplankton at a series of stations on a line from New York to Bermuda was approximately 4X as abundant over the slope area, outside the 200 meter line, as in the Sargasso Sea. The slope area, however, had but $\frac{1}{4}$ the zooplankton of the coastal area over the continental shelf. Here we see the contributions from the land producing some 16X as much plankton in coastal water as compared with mid ocean water in the Sargasso Sea. Also of significance is the fact that Clarke's results in 1937-38 showed significantly less plankton than in the catches of Bigelow & Sears in 1929-32. The latter followed 1928, the wettest year in the history of the Weather Bureau in New Jersey, whereas Clarke's observations were taken toward the close of the driest decade since the beginning of observations by the Weather Bureau in 1885.

Finally may we tie together the contributions; physical, biological and chemical, from the land to our coastal waters by a brief glance at the tidal flats of the Cape May shores of Delaware Bay where for the past two decades we have been attempting to solve some of the problems connected with the food and the feeding of oysters and of other molluscs.

The map shows Delaware Bay with some 30,000 acres of oyster planting grounds in Maurice River Cove and 20,000 acres of natural oyster setting grounds in the upper Bay. Investigation by the U. S. Coast and Geodetic Survey shows that deflection of the ebb tide to the right resulting from rotation of the earth, carries out along the Delaware coast approximately five times as much fresh water as along the New Jersey shore. On the succeeding flood tide, however, this same water again swings to the right, below Brandywine Shoal, and comes in upon the flats of Cape May. Our salinity studies here show that during a dry year the average salinity at low tide may actually exceed that at high tide, due to evaporation over the exposed flats during hot weather and the bringing in during flood tide of the

river flow which passed by Cape Henlopen on preceding ebb tides.

The Cape May flats, exposed up to nearly 3,000 feet in width during spring tides, support populations of diatoms and dinoflagellates far exceeding anything which your speaker has seen elsewhere in this country or in Europe. They approach at times the vast windrows of diatoms reported by Beeking and coworkers in 1927 for Copalis Beach, Washington. Pelagic diatoms are present at Cape May whenever the water covers the flats, but it is to the pennate diatoms living on the mud that our attention is now directed. Three species have predominated over the years; *Nitzschia closterium*, *Schizonema (Navicula) ramocissima*, and *Pleurosigma fasciola*. Nitzschia grown in the laboratory in dense cultures is reported to lose its frustule, becoming a naked cell. That this is not solely a response to laboratory conditions is shown by the fact that whenever this diatom appears in great numbers on the Cape May flats it is devoid of a frustule, a fact confirmed in our material by the late Dr. Albert Mann in 1932. Occasionally delicate empty frustules have been observed in the oyster's stomach contents. Dr. Ruth Patrick has shown me a slide of frustules of this diatom which had been boiled in acid. In these specimens, however, the terminal spines were much thicker than in the specimens here shown. These were very active, bending their spines and suddenly straightening out again to aid in driving the diatom through surrounding debriss. Is it possible under favorable conditions when Nitzschia is reproducing rapidly that it does not secrete a frustule?

Schizonema ramocissima, familiar to most of us as a diatom living in feathery tufts composed of secreted tubes, on the Cape May flats forms no tufts or tubes but secretes a film over the sand grains on the bottom. This helps to form a mat within which great numbers of diatoms and other organisms exist. What are the relationships of the bacteria here to the diatoms?
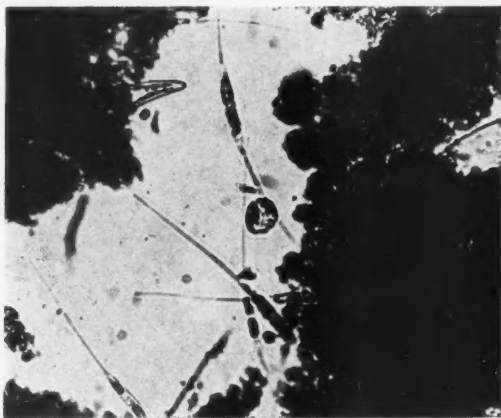

FIG. 5. Nitzschia closterium in the surface film on the Cape May tidal flats. These diatoms possess no demonstrable frustule the terminal spines aid the diatom in pushing its way actively through the mud.

May the blue greens Oscillatoria and Spirulina like Nostoc have the power to fix nitrogen and thus add to the sources of food not only for themselves but for the diatoms as well? We cannot doubt that the bacteria play an all important role in transforming organic detritus into nutrients available to both diatoms and blue green algae. We know that during the low tide when the mud in the sloughs is covered by not over 10 cm. of crystal clear water, the brilliant illumination results in such rapid photosynthesis that the water in and in immediate contact with the film becomes supersaturated with oxygen which soon forms a continuous mass of bubbles. These give buoyance to portions of the film sufficient to lift them off the bottom as the flood tide sweeps in over the flats. Wave action breaks up the mats while the undertow carries diatoms and other organisms in vast numbers off onto the oyster beds lying in deep water.

In calm very hot weather such numbers of dinoflagellates develop that the waters become bloody in appearance at the surface. In our experience these swarms have been almost exclusively the small spindle shaped *Amphidinium fusiforme*. One swarm, however, was composed of the much larger *Glenodinium*. With a sudden drop in temperature, accompanied by strong northwest winds, these dense populations of dinoflagellates have disappeared in part through being carried offshore by the undertow and in part through destruction by wave action. Within less than 48 hours after such an abrupt weather change the surface of the flats has been carpeted with a heavy film of Nitzschia or of Schizonema. Is this in response solely to a drop in temperature of approximately 2-4 degrees from a high of 30° C. obtaining during the dinoflagellate swarming? I do not think so, for both Nitzschia and Schizonema have been found in dense mats on the flats with temperature ranging from 32-34° C.

Dense swarming of dinoflagellates may be accompanied by wholesale death of fish. Is this due to production of a poisonous protamine as in the California mussel when feeding on a species of Gonyaulax, or is it the result of reduction in dissolved oxygen during the night or by dead dinoflagellates? Before answers to this and many a similar problem can be obtained we must obtain far more exact information on the role of dinoflagellates in marine ecology.

The heaviest diatom films have been seen on the Cape May flats during the summer and occasionally even in December and January. To ascribe the abundance at least of bottom diatoms to the effects of temperature alone is an oversimplification which only serves to hide the fundamental and somewhat

FIG. 6. Oxygen bubbles attached to diatom film on the Cape May flats at low tide. The darker area in the center is due to a heavy film of Schizonema beneath which many of the bubbles are trapped.

FIG. 7. Pleurosigma fasciola from diatom film on the Cape May flats. With four exceptions all of the diatoms in this figure belong to the same species, illustrating the dominance of individual types. At other times the dominant form may be Nitzschia closterium, Schizonema ramocissima, or even the rather rare Navicula complanata Grun, which may become abundant in October.

complicated changes which occur on the bottom. Are we not justified in the assumption that following the death and disintegration of naked dinoflagellates, bacterial action would in a few hours transform this finely divided protoplasm into food available to diatoms?

ZoBell (1946, pp. 75-76) states "that the abundance of bacteria in the water parallels the abundance of phytoplankton more closely than any other observed property of the water." His Figure 9, showing seasonal distribution of bacteria and phytoplankton in surface sea water at La Jolla for the year 1933, however, reveals the maximum numbers of bacteria occurring in from one to three months after the peaks of phytoplankton production, not parallel with them. Here is demonstrated a relationship of great fundamental importance, which applies to fixed algae and to Zostera as well as to phytoplankton.

Do we not have reason to question whether the disappearance of Zostera on our coasts was the calamity we formerly supposed it to be? The dense masses of this grass must have drawn heavily upon available supplies of nutrients which now are used and reused more rapidly by diatoms, dinoflagellates and other algae. To be sure the leaves of Zostera bore at times great numbers of epiphytic diatoms such as Achnanthes which contributed to the food available to plankton feeders. On the other hand hundreds of tons of eel grass torn loose by late summer and autumn storms were carried ashore or into shallow coves where they decomposed anaerobically with liberation of such large quantities of H_2s as to blacken nearby boats. Thick deposits were formed of black malodorous mud largely devoid of any animal or plant life save bacteria. Ostenfeld (1908, p. 37) refers to the paucity of marine life wherever

dead Zostera accumulated. He emphasizes the resistance of Zostera to putrefaction as contrasted with the rapid disintegration of algae. Each year there were removed from circulation great quantities of the compounds of carbon as well as of other essential elements. These, decomposing mostly anaerobically and in regions often far removed from the areas of chief productivity, may have resulted in a net loss of productivity. It is deeply to be regretted that we did not have, prior to 1930, precise data on the chemical and bacterial content of our coastal waters such as now is accumulating. It is suggested that studies in California waters where the western Zostera still thrives might prove very helpful. Here and there along the Atlantic Coast Zostera is struggling to regain a foothold and where it is successful we may yet have opportunity to evaluate the true role of this marine grass in the life cycles in our coastal waters. The future is rich in possibilities and may I close with the last sentence of Dr. ZoBell's book: "For the microbiologist with adequate training in chemistry, biochemistry, physical chemistry, general biology and hydrography the field of hydrobacteriology or marine microbiology is most promising being almost virgin, for research in pure and applied science."

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RELATIONS BETWEEN THE MOON AND PERIODICITY IN THE BREEDING OF MARINE ANIMALS

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RELATIONS BETWEEN THE MOON AND PERIODICITY IN THE BREEDING OF MARINE ANIMALS

INTRODUCTION

It can hardly surprise us, that a conspicuous celestial phenomenon like the moon, with its mysterious rhythmical waxing, and waning, has often set going the quaint wheel-work of human imagination, with the result that in many places on earth the moon played and still plays an important part in popular belief and superstition. The moon is said to affect weather-conditions, to influence the germination of the seed committed to the earth, to exert her influence on several marine animals, causing them to be "full" with the waxing, and "empty" or "spent" with the waning of the moon, and so on.

In modern times, science—going her way—is inclined to smile at these articles of popular belief, but anthroposophists, working in the borderland between mysticism and superstition, try to give them a scientific tinge, and do their utmost to stress the importance of the moon's influence on living beings. Still, every zoologist ought to know that there are some undeniable cases of lunar periodicity in the breeding of marine animals, the most spectacular case being the swarming of the Palolo worm at the moon's last quarter of October and November, in coastal waters of a few South Pacific islands. Scattered in literature, can be found a great amount of data, relating to the periodicity in the breeding of marine animals, and often a conspicuous correlation with the moon's phases cannot be denied. The different authors state the facts observed, but they seldom attempt to track and unravel the causal relations between moon and breeding, and often break down in their first effort to investigate this matter experimentally.

OYSTER INVESTIGATIONS (OSTREA EDULIS L.)

It was in quite an unusual way, that I came into contact with the phenomenon of lunar periodicity in the breeding of marine animals. The oyster farmers are faced with the problem of deciding when to plant cultch, so that it shall not be silted over, or covered with organic growth, before the oyster larvae are able to attach. A crisis in the Dutch oyster culture in the years following 1930, led to the establishment of a system of predicting the spatfall. Since 1935 the Government Institute for Fishery Investigations issues bulletins, once or twice a week in the course of the summer season. In these bulletins, are given, information and data concerning the number of larvae present in 100 litres of water, the growth of the larvae and the occurrence of "mature" larvae, also the water temperatures recorded, and the setting prospects (Havinga 1939, Korringa 1941). To this aim the checking of quantitative plankton samples, collected twice a day, provides the necessary data. For details concerning hydrographical conditions and a description of the methods of sampling and elaboration of our plankton samples, I refer to my paper of 1941, in which the data collected in the years 1935-1939 inclusive, are published in full. Within the near future, I hope to publish the results of observations and experiments carried out in the years after 1939.

It can hardly surprise us, that this wealth of information, collected in twelve consecutive years, reveals interesting aspects if treated in the proper way. During the course of my investigations, I have gradually gained more knowledge about uniformities in the production of oyster larvae. This in itself eventually led to the formation of a reliable system, whereby months ahead one can forecast the dates at which the greatest maxima in the production of oyster larvae can be expected, thus replenishing short term predictions based on plankton investigations. The latter, however, cannot be rendered superfluous, as larvae-production and setting are not always closely correlated, temperature and feeding conditions being of great importance in determining the rate of larval development.

To discuss extent and periodicity in the production of oyster larvae in our oyster district (the Oosterschelde, Holland) I present a few diagrams (Fig. 1, a, b, c, d), depicting the number of young oyster larvae (measuring 170-200μ) present in daily samples, procured from 100 litres of water, collected in the station Yersche Bank, in the centre of the Basin of the Oosterschelde. I have recorded next to the number of larvae, water temperatures and phases of the moon, but omitted large and mature larvae as well as spatfall data. Also noted are the average water temperatures for the periods April, May, first half of June, and at the foot of the diagram I depicted the number of mother-oysters present in the Oosterschelde, by adding the approximate number of oysters weighing at least 20 KG per 1000. One "oyster" represents 5,000,000 individuals.

The data for the years 1935 and 1936 are rather scanty, so our aim from 1937 onward was daily sampling; this took place from mid-June till late August. In the second part of August, being of minor importance, the samples were collected every other day, and for the rest only owing to stormy weather or the interference of Sundays, some samples are lacking. My diagrams show no gaps during the very difficult war years; this can be attributed to the great devotion to duty, shown by the officers and
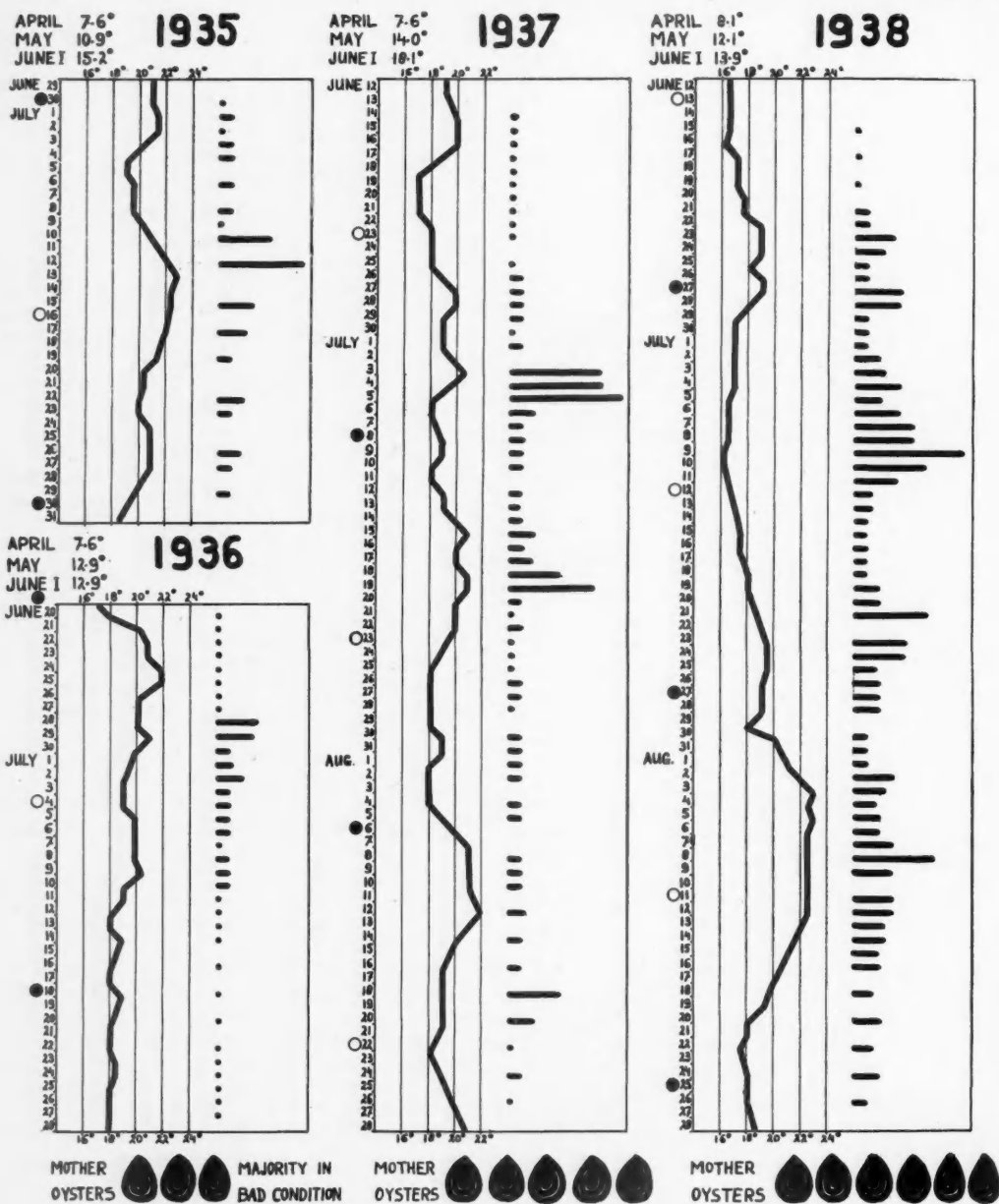
FIG. 1-A.   The production of oyster larvae in the Oosterschelde, Holland.

crews of the police boats of the Fishery Board of
the Zealand Streams.   In spite of an increasing
shortage of adequately equipped vessels, of steadily
decreasing fuel supplies, and of running the risk of
being killed by warfare, especially in the years 1943
and 1944, they managed to procure all the samples
I wanted, so that my series are complete, for which
I am very grateful.

THE EXTENT OF THE ANNUAL PRODUCTION OF LARVAE

When we compare the diagrams for the consecu-
tive years, the difference in the extent of the annual
production of oyster larvae is striking.   Maxima
being reached in the years 1939, 1945, 1946 and
marked minima in the years 1936, 1941, 1942, 1943.
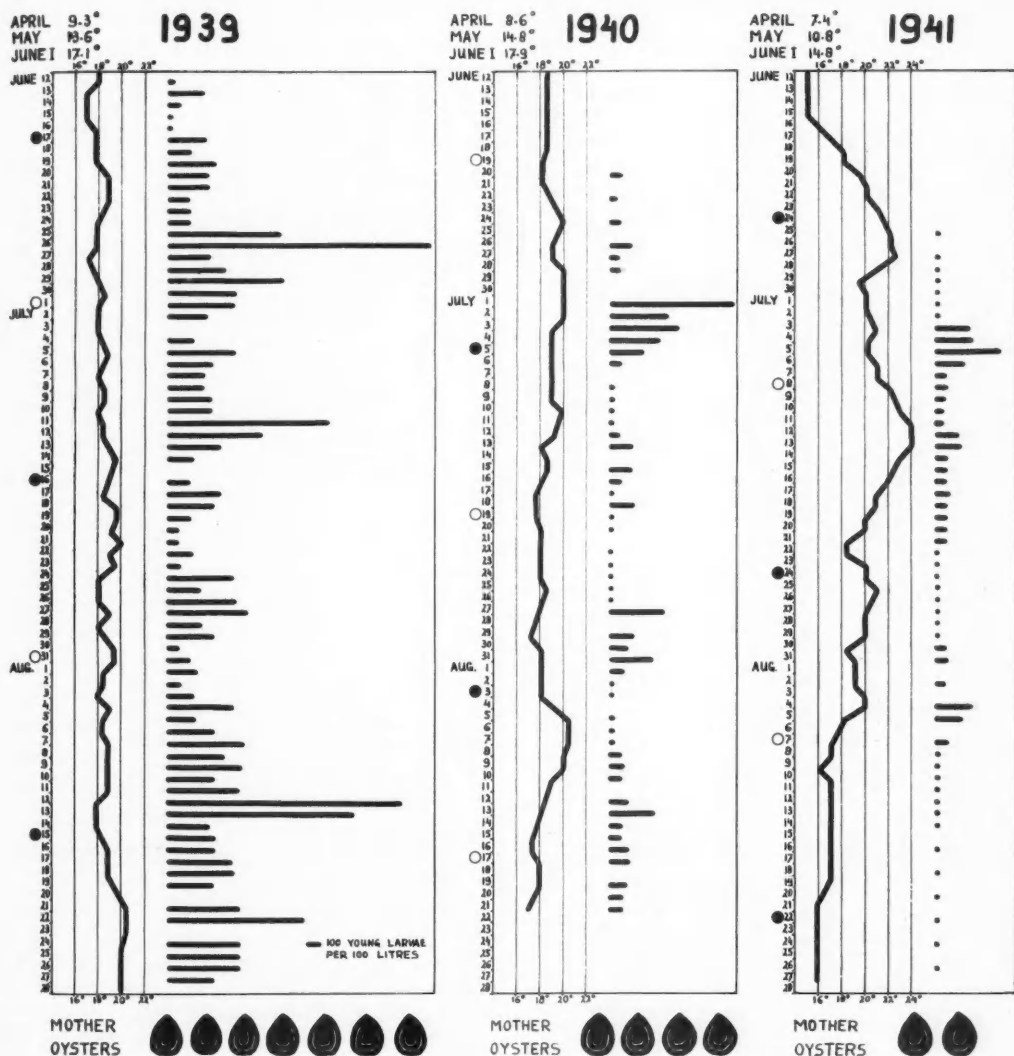What factors can be held responsible for the enor-

FIG. 1-B. The production of oyster larvae in the Oosterschelde, Holland.

mous differences, in the extent of the production of oyster larvae in the Oosterschelde? One glance at the diagrams convincingly shows, that it is the number of mother oysters which dominates in this respect. Water temperature in the course of the summer months, and in the period preceding spawning, apparently are of minor importance in determining the extent of the annual production of larvae, and the same holds good for possible differences in metabolic conditions. I hope to deal with this interesting phenomenon of great practical and theoretical importance in determining the extent of the annual production of larvae, and the same holds good for possible differences in metabolic conditions. I hope to deal with this interesting phenomenon of great practical

and theoretical importance in greater detail in a separate paper, which will be entitled "Uniformities in the Production of Oyster Larvae".

PERIODICITY IN SWARMING

A second glance at the diagrams makes clear, that the swarming of oyster larvae is not limited to a few days, but is distributed over several weeks. showing more and less important peaks. The diagrams do not reveal, however, any marked direct correlation between the periodicity of swarming and the course of the actual water temperature. A maximum of swarming may occur at high temperatures but, also at moderate or even low temperatures (July, 1938; June, 1946). Now swarming is only a delayed com-
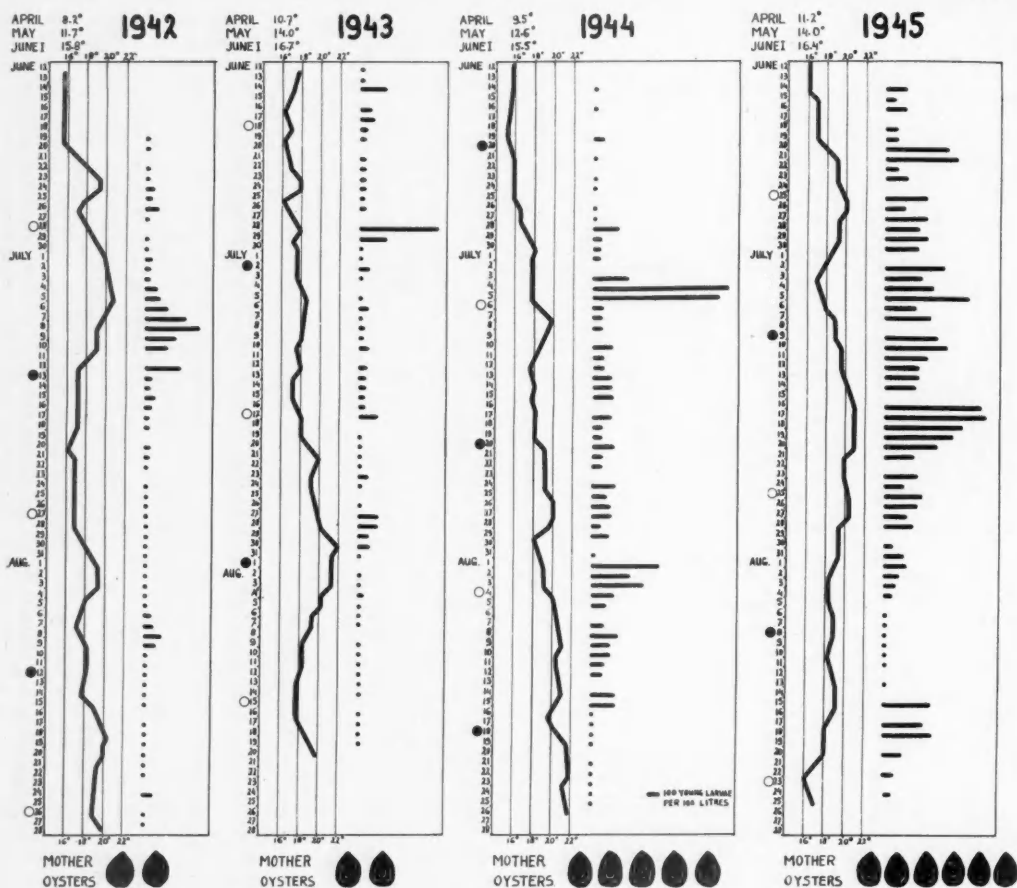
FIG. 1-C. The production of oyster larvae in the Oosterschelde, Holland.

pletion of the spawning process, by which the eggs are brought into the maternal mantle chamber. Spawning will have taken place about 8 days before swarming is observed.   Our diagrams convince us, however, that if it is a periodicity in spawning which governs the periodicity in the production of plank-tonic oyster larvae—and this is certainly the case—there is no correlation between the periodicity in spawning and the actual water temperature.   Like swarming, spawning may show a maximum at high temperatures or during an increase in temperature, but in many cases the temperature of the water has been moderate, decreasing, or low during spawning or the days immediately preceding it.

Ranson (1943) assumes that swarming is stimulated when there is thunder in the air: "Un temps orageux, avec basse pression atmosphérique, favorise cette expulsion."   This does not hold good for the Oosterschelde, however.   The Director of the "Koninklijk Nederlandsch Meteorologisch Instituut" at de Bilt placed at my disposal, a list of dates on which thunder has been observed in the Province of Zealand, in the summer season of the years 1935-1943.

This appeared to be the case in 28% of the days. Less than 28% of the dates, on which a maximum in swarming was observed, was characterized by thunder in the air, so the oysters apparently show no preference for this kind of weather to expel their larvae, and the same appeared to hold good for low air pressures.

A closer examination of the diagrams reveals the striking fact, that the large majority of maxima in the swarming of larvae can be located about 10 days after full or new moon!   In the intervening periods, swarming is not entirely kept down, but as a rule apparently is of little importance.   This leads to the conclusion, that spawning must have had its maxima roundabout the spring tides, which occur about 2 days after full and new moon.

Orton (1926) was the first to observe lunar periodicity in the spawning of *Ostrea edulis*.   He examined weekly samples of adult oysters.—which in fact is quite a crude method in checking breeding activities in large oyster populations—and located two important maxima in spawning at the full moon spring tides, in the year 1925.   This led him to the

1946

APRIL 10.3°
MAY 13.9°
JUNE I 15.5°

100 YOUNG LARVAE
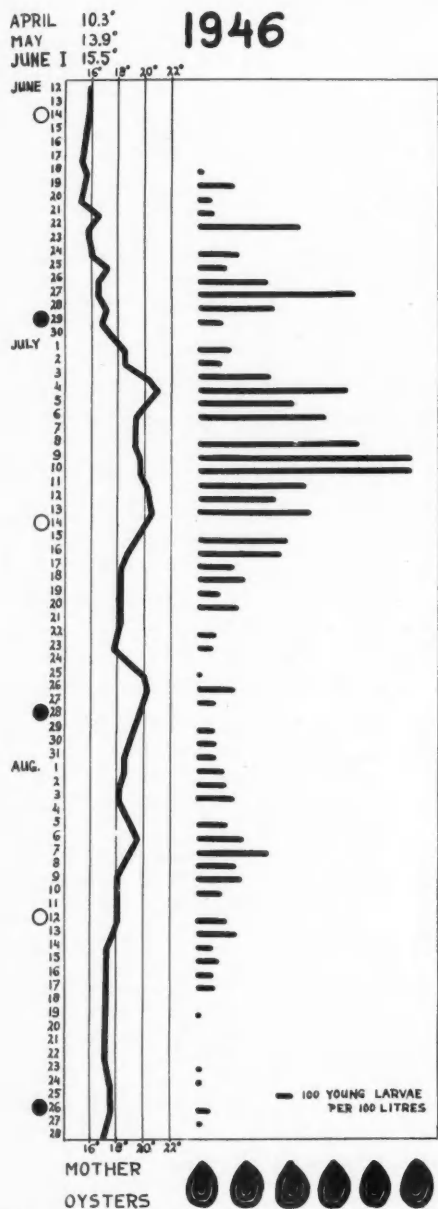PER 100 LITRES

MOTHER
OYSTERS

FIG. 1-D. The production of oyster larvae in the Oosterschelde, Holland.

conclusion, that his oysters showed a marked tendency to breed rhythmically at about the time of full moon. Orton (1937) did not observe this phenomenon in later years as clearly as he did in 1925.

My diagrams convincingly show, that lunar periodicity in the breeding of oysters really exists, be it that a full moon exercises the same influence as new moon. However, I would like to give Prof.

Orton credit for being the first to have lifted a tip of the veil, which covers this part of the many secrets of Nature.

It is not easy to establish the way in which the moon exercises her influence. As spawning maxima occur both at full and at new moon, the moonlight need not be taken into account and most probably it is the rhythm of the tides which does the trick. In the Oosterschelde the difference between high and low water is rather considerable and the greatest amplitudes can be expected at both of the spring tides. At spring tides the tidal range is about 3.9 metres, at neap tides 3.0 metres.

It certainly is not a rapid warming up of the water, during spring tides, while large parts of the tidal flats are exposed (though not exactly during the warmest part of the day), which exercises the direct action on the oysters. The weather is far too fitful on our coast to expect a rhythmical warming up of the water at spring tides; the diagrams help us to bear that out. The mother oysters in the Oosterschelde are not exposed at low tide, so exposure cannot be held responsible for the phenomenon concerned either.

Can it be a better penetration of sunlight, to the deeper parts of the oyster beds at the low tides which occur every fortnight at new and full moon? It is hardly conceivable. In the first place these low ebbs always occur before noon in the Oosterschelde, so that illumination of the sea bottom will reach the same value at spring tides as some days later, characterized by less low ebbs during the entering of steeper sunrays, so that sharp maxima in bottom illumination do not occur. In the second place, our fitful weather conditions know prolonged and irregular periods of overcast skies and spells of stormy winds, the latter causing a marked turbidity of the water in the Oosterschelde. Both these factors see that no exact rhythm in bottom illumination occurs, to be correlated with the marked rhythm in the production of oyster larvae. Moreover light is quite an indifferent factor in the life of the oyster. It was Loosanoff (1946) who showed us recently, that light or darkness do not affect *Ostrea virginica* in its feeding behavior.

In my idea the only reasonable factor which can be considered, as the intermediary between the rhythm of the moon and, the periodicity in the spawning of *Ostrea edulis*, are rhythmical differences in water pressure or possibly in current velocities. Of these two current velocity is the most irregular one, varying considerably from spot to spot, while the rhythmical changes in water pressure are in an absolute sense the same for every point below low-water-spring and those are the places where our mother oyster are to be found.

Is it absurd to assume that animals are sensitive to variation in pressure? Certainly not! Dijkgraaf (1941) showed that the fish *Phoxinus phoxinus* (L.) (Cyprinidae) is sensitive to variations in water pressure of 0.5-1.0 cm. and I only surmise that oysters—though they lack a swim-bladder and Weberian os-

sicles—are sensitive to differences about 100 times as large (tidal range 3.50 metres, difference springs and neaps 0.90 metres). So far we know too little about the oysters sensory perceptions.

Is it too bold to assume sensitiveness to rhythmical variations in a factor like water pressure? I don't believe so! There are quite a lot of well-established cases in Nature of sensitiveness to rhythmical impressions. Sexual periodicity and migration in birds, is largely influenced by the rhythmical lengthening of the days. And is not to the oyster the sequence of high and low water, of more importance than that of day and night? Many plants are very sensitive to the length of the day and show a marked reaction to its rhythmical impressions. The plant *Xanthium pennsylvanicum* appeared to be able to react to differences in the length of the day of the magnitude of half an hour (Hamner & Bonner 1938)!

I conceive that it is the rhythmical sequence of differences in water pressure from neaps to springs, and conversely, which exerts its influence on the oyster in the breeding period, so that maxima of greater and lesser importance in the extrusion of the eggs occur at spring tides (2 days after full and new moon), thus causing maxima in swarming about 8 days later. We still know very little about the precise mechanism. Is there any preference for extrusion of ripe eggs at spring tides or does the tidal rhythm affect egg-ripening? In the latter case the real point of attack should be sought earlier still. Or is it allowable to presume that both these factors in combination, cause an extrusion of eggs so well correlated with the tidal rhythm? It is conceivable that some hormonal cycle acts as an intermediary, as it does in periodicity in birds and plants, but so far no special investigations has been performed to bear that out.

It is a pity that it is not easy to carry out laboratory experiments to investigate this matter, as large numbers of oysters should be kept in perfect condition in large tanks, in which artificial tides, differing in rhythm from that which occurs in nature and with a range of about 3 to 4 metres, should be brought about. Experimental work would be much easier with any species breeding exclusively at spring tides, breeding activities dying down to zero in the intervening periods.

LONG TERM FORECASTING OF THE GREAT MAXIMUM

In the course of my investigations I became aware that every breeding season shows one great maximum in swarming next to one or more maxima of minor importance. Practically every year the most important maximum in swarming can be located in the last few days of June, or in the first decade of July, irrespective of temperature conditions. A few years ago I found a formula to predict the date at which the great maximum can be expected to occur, in the Oosterschelde, and the diagrams can be used to check the reliability of that formula: *"The big maximum in swarming is to be expected between June 26 and July 10, at about 10 days after full or new moon."*

To the oyster farmers it is of great importance to know when the major maximum in larval production is to be expected. In case water temperatures are favorable then (19° C. or higher still) an intensive spatfall can be expected to take place some 8-10 days later and only in case a cold spell interferes with larval development (e.g. 1938), setting prospects remain doubtful. In that case plankton investigations can help to establish whether or not any setting of economic importance can be expected. If not, the oyster farmers should not place their collectors till one of the maxima in swarming of minor importance is announced to make its appearance under more favorable weather conditions.

To the great surprise of our oyster farmers my formula has worked well in recent years and the larvae promptly appeared at the moment I had announced months ahead. I am glad I do not run the risk nowadays of being burned at the stake on suspicion of being a necromancer!

Whatever one thinks, it is my belief that the possibility to predict on long term both the extent of swarming and the date at which the bulk of the larvae are to be expected, this is of great practical importance to our oyster farmers. It fills up the gap in our knowledge on which Voisin (1931) laid his finger, stating: "Nous sommes donc encore obligé de constater toute l'obscurité qui entoure les différents facteurs d'influence qui régissent la ponte des huîtres. C'est pourquoi toute tentative pour prévoir à longue échéance l'époque et l'amplitude des pontes est, en état de nos connaissances, vouée à un échec."

We see that swarming usually sets in mid-June, but is of little importance then. Sometimes a maximum of minor importance (a so-called pre-maximum) appears about a fortnight ahead of the big maximum, especially when the latter is to be expected in the last few days of the period mentioned in the formula. One or two periods of fourteen days after the occurrence of the big maximum, peaks of minor importance appear and in the second half of August breeding activities usually die down.

To depict the established uniformity in the production of oyster larvae in the abstract I designed a special diagram (Fig. 2), in which the data for the years 1937-1946 inclusive are assembled. To this aim I computed the figures for every year under consideration on the same base, thus eliminating the influence of differences in the annual extent of the production of larvae. Thus the figures for the years 1941, 1942, 1943 remained unchanged, those for the year 1937 were multiplied by 3/5, further 1938 × 3/8, 1939 × 3/18, 1940 × 3/5, 1944 × 1/2, 1945 × 1/4, 1946 × 1/4. Moreover I interpolated the data lacking owing to the interference of Sundays and I made one slight correction, viz., for the big maximum of 1944, which I antedated 2 days because it came too late owing to unusually low temperatures during incubation. Then I added them up, seeing that the spring tides always corresponded with each other,

TABLE 1. Maxima in the swarming of *Ostrea edulis* at the station Yersche Bank, Oosterschelde, Holland in the years 1935-1946 inclusive.

Year	Major maximum		Minor maxima	
1935......	11 July	N.M. + 11		
1936......	28-29 June	N.M. + 9-10		
1937......	3-5 July	F.M. + 11	18-19 June	N.M. + 10-11
			18 July	N.M. + 12
1938......	9 July	N.M. +12	21-23 July	F.M. + 10
		(incubation at 17°)	7 August	N.M. + 10
1939	26 June	N.M. + 9	11 July	F.M. + 10
			26-27 July	N.M. + 10-11
			12 August	F.M. + 12
1940......	1 July	F.M. + 11	13 August	N.M. + 10
1941......	3-5 July	N.M. + 10	4 August	N.M. + 10
1942......	7-8 July	F.M. + 10	8 August	F.M. + 12
1943......	28 June	F.M. + 10	14 June	N.M. + 10
			27-28 July	F.M. + 10-11
1944	4 July	N.M. + 14	1 August	N.M. + 11
		(incubation at 16°)		
1945......	5 July	F.M. + 10	20-21 June	N.M. + 10
	16-17 July	N.M. + 7-8	17 August	N.M. + 9
		(incubation at 21°)		
1946......	9-10 July	N.M. + 10-11	27 June	F.M. + 13 (incubation at 16°)
			7 August	N.M. + 10

and placing the new or full moon mentioned in my formula on the same height. The result clearly shows a pronounced maximum about 10-11 days after the moon mentioned in my formula, two peaks of minor importance one and two fortnights later, the slight peak of the pre-maximum early in the season and a slight post-maximum near the conclusion of the breeding season. With the exception of the major maximum one or more of the maxima may be missing in the different years.

It is very remarkable that the formula seems to hold good for all the years under consideration, though water temperatures in the weeks and months preceding swarming, are by no means always the same and may even show quite considerable differences (Table 2).

Temperature appears to be of far less importance in determining the dates at which swarming takes place, than is often assumed. Though practically nobody still clings to Leenhardt's idea (1924), that swarming is a function of temperature[1]), many investigators believe that a time-caloric period determines when swarming sets in, following the footsteps of American scientists working with *Ostrea virginica*. The supposed predomination of temperature in determining the beginning of spawning, seems to become discredited elsewhere too, for Dr. Loosanoff of the Milford Biological Laboratory (U.S.A.) wrote me recently (1945): "We have learned that the so-called critical spawning temperature of 20.0° C. is nothing but a myth."

[1] Navaz y Sanz (1942) appears to assume a close correlation between the course of water temperature and swarming activity: "La presencia de larvas libres en el agua es posible a la temperatura de 15°, pero la emisión no se da con cierta abundancia más que a partir de los 18°, límite inferior también para la fijación de las larvas, teniendo lugar las fuertes emisiones y abundante fijación del enjambre entre los 20° y los 22°."
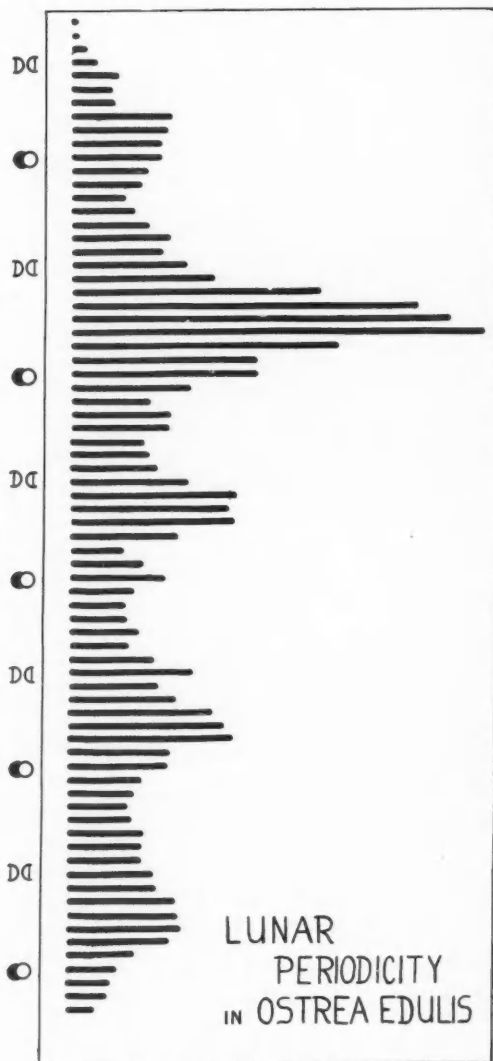

FIG. 2. The production of oyster larvae in the Oosterschelde, Holland, in the abstract.

Our diagrams clearly show that the tidal rhythm and a fixed period in the summer season are far more important in bringing about a periodicity in the production of oyster larvae than water temperature.

THE LOCATION OF THE BREEDING PERIOD IN OSTREA EDULIS

It is not my intention to deny that temperature is a very important factor in the oyster's biology. Did we only have at our disposal the data depicted in the accompanying diagrams, we could too easily be led

TABLE 2. Water temperatures in the Oosterschelde, Holland, in spring and autumn.

Year	April	May	June 1 (1st half)	Sept. 11 (2nd half)	October	November
1934				16.6	12.0	6.4
1935	7.6	10.9	15.2	14 3	10.6	7.0
1936	7.6	12.9	12.9	15.2	9.2	5.3
1937	7.6	14.0	18.1	15.8	12.7	7.3
1938	8.1	12.1	13.9	17.8	12.7	9.8
1939	9.3	13.6	17.1	17.6	11.4	7.9
1940	8.6	14.8	12.9	14.0	9.2	7.7
1941	7.4	10.8	14.8	16.8	13.1	6.2
1942	8.2	11.7	15.8	15.8	13.4	8.6
1943	10.7	14.0	16.7	15.7	13.1	8.0
1944	9.5	12.6	15.5	14.8	11.9	7.2
1945	11.2	14.0	16.4	16.4	13.7	8.5
1946	10.3	13.9	15.5			
Average 1920-1940	8.5	13.3	16.5	15.6	12.1	7.1

Spring-surpassing of the 10° C. level on an average on April 25th.
Spring-surpassing of the 15° C. level on an average on May 26th.
Autumn-dropping below the 15° C. level on an average on October 2nd.
Autumn-dropping below the 10° C. level on an average on November 3rd.

to the conclusion that it is only a fixed period of the year which counts and that water temperature is quite irrelevant in the breeding of the oyster. The big maximum always appears in due time, at the most, a few days later in case incubation is performed under unusually low temperature conditions (e.g. 1938, 1944). A colder or a warmer spring apparently cannot subvert the rhythm (Tables 1, 2). May and the first half of June may be colder or warmer, but the moment water temperature surpasses the 15° C. level—which is generally considered to be the critical level for reproductive activities in our oyster (Orton 1920, 1927)—does not diverge very much in the different years, as can be derived from Table 3.

TABLE 3. The 15° C. level in the spring.

Year	Water temperature surpassing the 15° C. level.	Number of days between surpassing of 15°C. level and the occurrence of the full or new moon at which the big spawning maximum occurs.
1935	30 May	30 days
1936	12 June	7 days
1937	22 May	31 days
1938	6 June	21 days
1939	23 May	24 days
1940	28 May	21 days
1941	7 June	17 days
1942	3 June	25 days
1943	28 May	20 days
1944	30 May	21 days
1945	1 June	24 days
1946	7 June	22 days

It is only in the year 1936 that a very short period (7 days) elapses between the surpassing of the 15° level and the occurrence of the spring tide, at which the great maximum in spawning took place. Is it too bold to assume that this fact contributed

to bring about the disappointingly small extent of the production of larvae in 1936?

There are two considerations, which force us to admit that temperature conditions are involved in determining the approximate beginning of the breeding season in *Ostrea edulis*. In the first place it proved to be possible to force the oysters to start breeding at a far earlier date, than they are inclined to do on the local oyster beds. This result has been accomplished by Dr. Dannevig and his assistants in the laboratory of Flødevigen, Norway (in litt. 1946, 1947), by placing the oysters early in spring, in heated aquaria (20-25° C.), which resulted after about 5 weeks in the production of healthy, normal larvae. In the second place, the further south in Europe, the earlier reproductive activities appear to start. In the important oyster region of the Morbihan (Brittany, France) situated some 500 km south of the Oosterschelde, oysters tend to concentrate swarming in the same period at the end of June and the first days of July, as in the Oosterschelde. The data published by French investigators (Boury, Voisin, Herman) do not allow us to establish, whether or not, a neat periodicity in the production of larvae occurs in Brittany. The tidal range being of the same magnitude as in the Oosterschelde, I would not be surprised if it did. In the basin of Arcachon, however, situated in the extreme Southwest of France, reproduction starts about a fortnight earlier than in Brittany and Holland, showing its major maximum in June. The data published by Borde and Ladouce so far are not sufficient, however, to give a decisive answer to the question whether periodicity in reproduction prevails in the basin of Arcachon. Still further south, in the lake of Fusaro near Naples in Italy, breeding starts as early as March, finding its height in April or early May and gradually dying down as summer proceeds (Mazzarelli 1924).

This all fits well in Orton's theory (Orton 1920) that there are minimum breeding temperatures, which should be a physiological constant for the species. I do not fully agree with Orton's statement, however, that the oyster begins to breed at a temperature of 15-16° C. and continues to breed so long as the temperature remains above this figure. We have seen already that in Holland some time elapses after the surpassing of the 15° C. level before the larvae appear in the water in quantities of some importance, the bulk of the eggs being laid some 22-26 days later and expelled as larvae only some 30-34 days after the reaching of this critical temperature. That breeding carries on so long as the temperature remains above 15° C. level, is only true in a very general sense. A few incubating oysters and some occasional larvae may be found late in August and in September. As a rule breeding activities die down in the second part of August, long before the temperature drops below the 15° C. level, the year 1939 being the only notifiable exception so far as we are aware. In September, when water temperatures may be as high as 19 or 20° C., at least in the first decade, oyster

larvae always are extremely scarce. The same principle holds good for other oyster regions; e.g., at Naples, where summer temperatures are high, but breeding in oysters had its height in April and is of little or no importance later on.

CONCLUSIONS IN RE OSTREA EDULIS

The extensive data concerning periodicity in the production of oyster larvae in the Oosterschelde, analyzed and considered may lead to the following conclusions.

1. The extent of the annual production of oyster larvae is mainly governed, by the number of mother oysters present in the area concerned.

2. Egg-ripening in Ostrea edulis probably requires temperatures above the 15° C. level. Breeding does not start automatically as soon as the water temperature surpasses this level, but some time has to elapse before large scale breeding activities can be expected to occur. As long as water temperature remains above the 15° C. level, the sequence of events is not influenced by temperature conditions. Larvae-production increases, reaches its height, next decreases again in its intensity and eventually dies down, often long before the water temperature drops anew below the 15°C. level.

3. The adjustment of the events during the breeding season, resulting in a marked periodicity in breeding, included the appearance of a major maximum, located in a short well-defined period of the summer-season, is called forth by the rhythmical sequence of spring- and neap-tides. Probably rhythmical differences in water pressure are the agent in this. Spells of warm or cold weather do not subvert this rhythm. A practical application of this knowledge, is the long-term prediction of the date at which the major maximum in the production of larvae will occur in the region concerned.

4. Swarming itself, being only a delayed completion of the spawning process, takes place as soon as the larvae have been incubated properly. The incubation process takes about 8 days, at most a few days more if incubation is performed at unusually low water temperatures. Swarming may be observed at day or night, at high or low water, during ebb or flood, in fair or stormy weather, at high and low temperatures. As far as we are aware, external conditions do not influence noticeably the swarming process.

PERIODICITY IN BREEDING IN OTHER SPECIES OF OYSTERS

We can be very brief in discussing periodicity in breeding in other species of oysters. Extensive observations and experiments have been carried out with the American species Ostrea virginica and O. lurida. The latter is a near relative of Ostrea edulis, and plankton investigations, recently proved to be a great help in predicting setting intensities. The data published so far are not sufficient to decide whether or not periodicity in swarming correlated with the tidal sequence occurs.

The behavior of the larvae of the non-incubatory species Ostrea virginica appears to be still quite puzzling in many respects, and plankton investigations did not always yield useful results. Spawning tends to occur simultaneously in a great number of individuals in this species. Galtsoff's clever experiments (1930, 1932) showed that a mutual stimulation by chemical substances present in the sex-products are the intermediary in this phenomenon. We should assume, however, that only oysters of which the ripening of eggs or sperm is well-advanced, can participate in simultaneous spawning. Nothing much has been published so far about a possible rhythmical ripening of these oysters, correlated with the sequence of springs and neaps. We should be aware, however, that practically everywhere on the North-American East-coast, with the exception of Canadian waters, tidal ranges are of a far smaller magnitude than that in the Oosterschelde. The time-caloric period, long considered as a reliable factor inducing egg-ripening in Ostrea virginica, has become somewhat discredited in recent time, as has been stated.

PERIODICITY IN BREEDING CORRELATED WITH THE TIDAL SEQUENCE IN ANIMALS OTHER THAN OYSTERS

Using our extensive, well-analyzed and duly synthesized data about breeding periodicity in Ostrea edulis as a base of operations, it was possible to make a fruitful ramble through literature, and to reach a better understanding of many scattered observations. As a rule, the observations do not cover a great number of years and never reach the frequency of sampling of our basic material, and thus often make an analysis quite difficult, but no one is to blame for this. Procuring and elaborating quantitative samples over a long period, is a time-devouring and expensive matter and I want to have it clearly understood, that I did not carry out my investigations on oyster larvae in a special pursuit of a possible rhythm in the oyster's breeding activities. In fact the uniformities dealt with above were only detected after several years of routine spatfall prediction.

We can characterize rhythmical breeding in our basic material, Ostrea edulis, concisely as follows:

1. OSTREA EDULIS L.

(Mollusca, Lamellibranchiata).

Region of investigation Oosterschelde, Holland. Tidal range spring tides 3.9 metres, neap tides 3.0 metres. Breeding period mid-June till late in August. Maxima in spawning at both full and new moon spring tides. Expulsion of larvae 8 days later, at any time of the day; major maximum in swarming between June 26 and July 10, 10 days after full or new moon.

2. *LEURESTHES TENUIS*

(Pisces, Atherinidae).

Region of investigation the coast of California, U.S.A., notably the San Pedro area; tidal range springs 2.3 metres, neaps 1.4 metres; investigators Thompson (1919) and Clark (1925).

This little fish, locally called the "grunion," displays most remarkable breeding habits. It deposits its clusters of eggs in the sand of the beach, quite near the high-water mark of the spring tide. The fish swims ashore in great numbers (a "run") at night, shortly after the moment of high water. They can easily be observed in the act of mating and egg-deposition as they are sometimes uncovered on the wet sand for a few moments. Afterwards the eggs deposited by the fish in a self-dug hole in the sand, are covered by new layers of sand supplied by wave-activities and remain for about a fortnight in the sand till the erosion brought about by the high tides of the next spring tide digs them out again, at which moment they hatch.

The grunion's spawning season starts as early as March, and dies down in the middle of summer, having its height in April and May. The "runs" can be observed during the 2nd, 3rd, or 4th night after full and new moon, but curiously enough it is only the full moon "run" which has drawn the attention of a greater public. Large crowds visit the beach on that occasion to enjoy the pleasure of catching the spawning grunions, which has resulted already in a rapid numerical decline of this interesting species. Clark made it clear, that the new moon "run" is less easily observed not only because of a scantier illumination, but also because the time of high water comes later in the night at new moon springs than at full moon springs, showing a difference of an hour at least.

Thompson gives a vivid description of the spawning habits of the grunion, while Clark made an accurate study of the ovaries, in a great number of samples collected at regular intervals. Clark clearly showed that the individual fishes take part in reproduction every springtide, so at fortnightly intervals. It appeared to be a clear-cut case of rhythmical egg-ripening correlated with the tidal sequence and Clark could track the development of the fortnightly batches of eggs. Egg-ripening appeared to require about 15 days.

Corresponding with our oyster data, we can characterize Leuresthes' breeding habits and breeding periodicity concisely as follows: Breeding season from March till mid-summer, having its height in April and May. Spawning at fortnightly intervals, each time 1-3 days after full and new moon, this in close correlation with rhythmical egg-ripening. I believe that here too rhythmical variations in water pressure brings about a synchronization of egg-development and the sequence of neaps and springs. The tidal range and the differences between springs and neaps are of a quite considerable magnitude. The complicated spawning act itself is performed only at night and notably during the hour after the water's highest level.

3. *ENCHELYOPUS CIMBRUS* (L.)

(Pisces, Gadidae).

Region of investigation Passamaquoddy Bay, on the Canadian East coast; tidal range springs 8 metres, neaps 5 metres; investigator, Battle (1930); observations in 1927 and 1928.

This fish is living near the bottom of Passamaquoddy Bay at a depth of about 30 metres, where the water is of an equable temperature of about 9° C. during the spawning season. The fish breeds in the summer season, over a period of several months, but having its height in July and August. Later in the season, although the temperature may be further elevated, the number of ova decline. The eggs of this fish are pelagic, and can be found in great numbers in the surface layers of the water. Battle's sampling showed that there are marked maxima in spawning at both of the spring tides—these being of about the same magnitude in the years under consideration—and minima roundabout the neaps, though breeding activities do not reach the zero level then. Differences in illumination (the fish living at a depth of about 30 metres) or in temperature being out of question, Battle concludes, that the chief factor causing the rhythm is probably tidal.

We conclude that this case fits in well with the case of *Ostrea edulis* and *Leuresthes tenuis* already discussed:

A breeding season of several months with its height during July and August, and periodicity with maxima at both of the spring tides, most probably correlated with rhythmic variations in water pressure. The spawning act itself appeared to take place to some degree at any time of the day, but to a greater extent in the early morning.

4. *LITTORINA NERITOIDES* (L.)

(Mollusca, Gastropoda).

Region of investigation Plymouth, on the South-coast of England; tidal range springs 4.2 metres, neaps 1.8 metres; investigator Lysaght (1941); observations in 1935 and 1936.

Lysaght established that the main breeding period of *Littorina neritoides* lasts from September to April, egg-production showing a marked minimum in June, July, and August. By examining tow nettings collected at the Plymouth breakwater from November 29, 1935 to May 1, 1936, Lysaght could check the occurrence of egg-capsules of this species. He found the highest figures at spring tides. "The strongest indication of the presence of a fortnightly rhythm in the spawning habits of the species, is shown by the breakwater samples. Although many of the snails there live permanently in water, egg-capsules were abundant in only three out of seven sets of samples that were examined, and these three were taken when the moon was new or full. This is of particular interest, as during the winter and spring the sea usually sweeps over the breakwater twice a day."

Though some caution should be exercised in drawing conclusions on the factors bringing about periodicity in reproduction in any species living above the low water mark, it is quite probable that *Littorina neritoides* ought to be ranged in our list of animals showing periodicity in breeding correlated with the tidal sequence.

Characterization: breeding period from September to April, with spawning maxima at both of the spring tides, even there where many of the snails live permanently in water.

5. *PLATYNEREIS DUMERILII* Aud. & M. Edw.

(Annelida, Polychaeta).

Region of investigation Concarneau, Brittany, France. Tidal range springs 4.2 metres, neaps 2.1 metres; investigators Fage (1933), Fage & Legendre (1923, 1923a, 1927), Legendre (1935); observations in 1923.

Inspired by the ancient and approved method to allure and catch anchovy in the dark of the night with the aid of artificial light, Fage carried out some experiments in the Mediterranean near Banyuls (France, near the Spanish border). The results were surprising. Herds of small marine invertebrates were allured by the light he suspended under the surface of the sea, among which many species which have never been observed to lead a pelagic life during the daylight hours. Fage observed several species of polychaetes displaying their quaint nuptial dances in the radiation of his lantern.

After these preliminary investigations Fage & Legendre carried out one of the finest sets of ecological field observations known to me. During an entire year, their small boat left the harbor of Concarneau (Brittany, France) at sunset, once a week, at new moon, first quarter, full moon, and last quarter. In a well-selected station in the Bay of Concarneau they made anchorage after which a powerful acetylene lamp, fitted in a buoy, was placed in the sea. During the first few hours after sunset one aimed at catching quantitatively the many invertebrates that made their appearance in the lantern's radiation and at observing the behavior of these animals. The light of the lamp did not evoke the animals to approach the surface of the sea, but it merely concentrated many of the species that had left their shelter and swam actively in the surface layers during one or more well-defined hours of the night, according to the species concerned.

Fage & Legendre stuck with great perseverance to their plan to carry on with these observations during an entire year, and they were there even in winter in cold nights, in rain and sleet, and only a few times stormy weather prevented them from leaving the harbor. They had the good luck, that the year 1923, in which they carried out this set of observations, was characterized by many days of calm weather: "Les periodes de calme nombreuses permirent un grand nombre de pêches, systématiquement pratiquées aux moments des quartiers de la lune." But setting aside favorable weather conditions, only a great devotion to the enormous task Fage & Legendre set themselves, could lead to their collecting a most valuable and complete set of observations, though this made high demands on their time and on the little money available. They caught Polychaeta, Amphipoda, Ostracoda, Cumacea, Isopoda, Mysidacea, and Pycnogonida and many species only made their appearance during a well-defined part of the year and often showed their maxima at special phases of the moon.

The most remarkable features in their observations certainly are the nuptial dances of polychaetes, among which those of *Platynereis dumerilii* are most spectacular of all. From May to September incredible numbers of this polychaete worm were observed around the lamp, carrying out their nuptial dances, but only at the first and last quarter, the species being absent in the full and new moon catches (Fig. 3). The worms made their appearance some time after sunset, reached a maximum in numbers and activity, and sensibly decreased in numbers before midnight. This marked rhythm cannot be caused by variation in moonlight, as there was moonlight during sampling at first quarter, but none during sampling at last quarter (the first few hours after sunset), while overcast skies did not prevent their arrival. In fact the investigators often observed swarming of Platynereis even "quand l'astre est caché par d'épais nuages" (Legendre 1925). Fage & Legendre confine themselves in stating the fact of rhythmical appearance of Platynereis in enormous numbers, at first and last quarter during the summer months, without being able to give a plausible explanation of the phenomenon: "L'existance des rythmes lunaires n'est done plus douteuse, bien qu'il soit impossible d'en donner l'explication" (Legendre 1925).

I am strongly inclined to believe, that the rhythm in *Platynereis dumerilii* is of the same nature as that discussed in the oyster *(Ostrea edulis)*, and that in other species of marine animals showing maxima in reproductive activity twice in the lunar cycle, and correlated with the rhythmical sequence of differences in water pressure.

An analysis of Fage & Legendre's methods can lead to criticism as to the absolute reliability of their figures. In the first place they point at sharp peaks next to zero or nearly-zero minima in the appearance of Platynereis, but as they only sampled once a week, at new moon, first quarter, full moon, and last quarter, their statement: "comment tous ces animaux font-ils pour être prêts le même soir?" (Legendre 1925), is not quite correct. For, the possibility remains, that one or even more nights preceding or following the nights of first and last quarter, considerable numbers of this polychaete worm made their appearance in the sea's surface layers, to perform their nuptial dance, with Fage & Legendre's superintendence. This criticism only leads to some doubt as to the sharpness of the maxima, but the impressive rhythm itself remains.
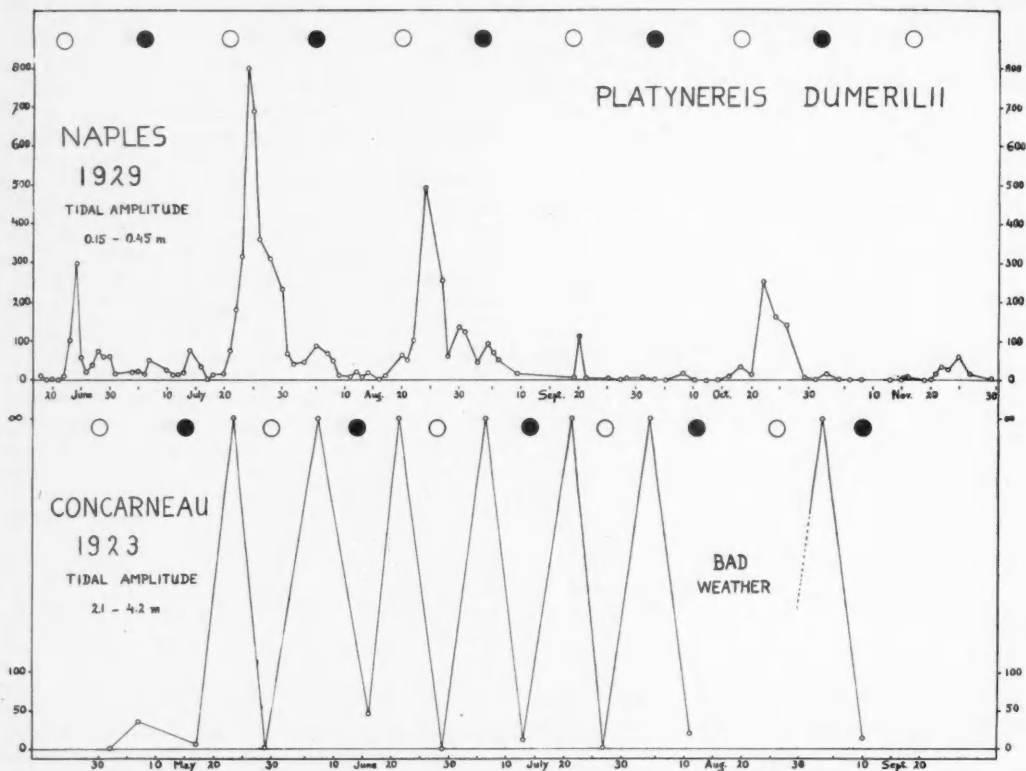
FIG. 3.   Periodicity in swarming in Platynereis dumerilii Aud. Edw.   At Naples (above) after Ranzi.   At Concarneau (below) after Fage and Legendre.

In the second place we can wonder whether or not, current velocities influence this worm's appearance. As observations are not carried out at exactly the same phases of the tidal cycle (e.g. at high water or at low water), but in fact during the first few hours after sunset, current conditions will differ quite a lot, during the observations in the consecutive weeks, taking into account that the tidal range is quite considerable at Concarneau.   It is impossible, however, to ascribe the rhythm in Platynereis to differences in current velocities during the hours of observation, for Fage & Legendre always left the harbor at sunset.   The sunset takes place at quite different hours of the night in the months of May, June, July, August, and September.   So observations during first and last quarters were not performed at exactly the same stage of the tidal cycle in the course of the summer season, on the contrary, marked differences in current velocity during observations could easily be shown (cf. the diagram in Fage & Legendre 1927).   So it is my belief, that it is not a difference in current velocity which leads to the establishment of the rhythm in Platynereis, and that we need not assume Platynereis swarms in great numbers during full and new moon too, but then in later hours of the night.

Of course, we should like to possess data collected during all the hours of the night, from sunset till sunrise, and that every day of the week during one or more years, but this aim could only be reached if an automatical apparatus to allure and catch the animals, could be devised.   Of course we should not reproach Fage & Legendre because their frequency of sampling is insufficient and that they did not stay out the whole night, on the contrary we ought to be grateful, that they collected the wealth of data displayed in their publications.

We can characterize Platynereis' behavior at Concarneau, concisely as follows: breeding season from May to September; maxima in swarming, most probably called forth by rhythmical ripening closely correlated with the sequence of springs and neaps, at the first and last quarters, in the first few hours after sunset.   Nuptial dances in the first few hours after sunset.

6. *ODONTOSYLLIS PHOSPHOREA* Moore
(Annelida, Polychaeta).

Region of investigation Departure Bay, Nanaimo, B.C., on the Pacific Coast of Canada; tidal range springs 3.5 metres, neaps 2.0 metres; investigators Potts (1913), Fraser (1915); observations 1911-1914.

Potts witnessed swarming and nuptial dances of *Odontosyllis phosphorea* in Departure Bay at sunset on August 15th 1911 (at the last quarter) and on August 18th 1912 (at the first quarter).   Fraser completed his observations in the years 1913 and

1914. He affirmed Potts' statement that swarming only takes place at sunset "from sunset or possibly a little before it, until almost dusk, that is for a period lasting from half an hour to an hour, they appear at the surface, whether the sun sets early or late." The nuptial dance was never observed by Fraser in case rough weather prevailed. He was in a position to provide us with the following data:
Swarming of Odontosyllis phosphorea in Departure Bay:

Dates	Remarks	Phases of the moon
15/16 August 1911	Potts	Full moon + 6/7
18 August 1912	Potts	New moon + 6
5 September 1912		Full moon + 9
21/22 August 1913	plentiful	Full moon + 5/6
6 September 1913	numerous	New moon + 6
30/31 July 1914	numerous	New moon + 8/9
14 and 19 August 1914	numerous	Full moon + 9 and + 14
29 August 1914	plentiful	New moon + 8
5 September 1914	plentiful	New moon + 15
21 September 1914	very plentiful	New moon + 16
6/8 October 1914	numerous	Full moon + 14/16

On many occasions absence of swarming could be demonstrated at interjacent dates. Fraser concluded: "it will be seen at a glance, that there is no indication of periodicity in the swarming, but apparently it may take place at any time within a period of three or four months." Though definite conclusions can only be drawn from a more ample material, I do not share Fraser's pessimism and I should like to deduce from Fraser's data that swarming of Odontosyllis usually takes place 6 to 9 days after full or new moon and that only in the last part of the breeding season of 1914 (September, October) swarming was delayed to about 15 days after full or new moon. Following up our discussions I see Odontosyllis' periodicity as a result of rhythmical ripening of the worm's sex glands in close correlation with the rhythmical sequence of springs and neaps. Spring tides most probably initiate egg-ripening and it is not improbable that the number of days required for the maturation process, is dependent on temperature conditions. The latter may have been less favorable in September and October of 1914, thus causing the delay mentioned above. More observations, including temperature readings, are required to bear out whether or not my hypothesis holds good in this particular case.

Provisionally I prefer to characterize Odontosyllis' rhythm concisely as follows: breeding season from the end of July to the beginning of October. Maxima in swarming, most probably called forth by a rhythical maturation closely correlated with the sequence of springs and neaps, at about 6-9 days after full and new moon; in September and October 1914 delayed to about 15 days after full and new moon. Nuptial dance at sunset, for a period lasting from half an hour to an hour.

7. CERATOCEPHALE OSAWAI Izuka

(Annelida, Polychaeta).

Region of investigation Sumida River, Tokyo, Japan; tidal range springs 1.4 metres, neaps 1.1 metres; investigator, Izuka (1903).

Immature worms (atocous form) of this species occur in great abundance between the tide marks along the Sumida River, on which Tokyo is situated. With the flood tide, irrespective of the hour of the day, they leave their retirement and creep about on the bottom. They are very active and voracious, feeding on various aquatic animals and plants. Late in the year metamorphosis can be observed, during which the anterior part of the worm grows stouter and becomes filled with sexual products, afterwards. The posterior 2/3 of the body shrivels up and is eventually cast off. Thus epitocous worms come into being. They can leave their burrows, to start their nuptial dance in the surface layers of the water. While swimming about they are easily attracted by light; observations in an aquarium showed Izuka that a single candle is sufficient to allure them.

Local fishermen knew that swarming in this species can be expected in October and November in short periods at full and new moon. Izuka was in a position to check this empirical knowledge and demonstrated that "swarming takes place during nights closely following the new and the full moon in October and November." Swarming activity is then restricted to a few consecutive days only. Izuka observed very dense swarms on October 9, 1896 during which "one could not dip his hand into the water without touching some." Swarming began about 9 p.m. and two hours later there were none to be found. Izuka did not confine himself to the observation of swarming maxima, but also collected samples of the worms living in the mud flats, at frequent intervals. Thus he was able to demonstrate, that epitocous or half-epitocous forms could only be found the last few days preceding swarming: "After each swarming period the transitional half-epitocous forms totally disappear for a time from among the worms collected in the river bottom."

Thus Izuka's data fit in remarkably well with the cases discussed as *Ceratocephale osawai* shows without doubt a rhythmical egg-ripening in close correlation with the sequence of neaps and springs.

Characterization: breeding period October and November. Clear-cut swarming maxima at new and full moon. Rhythmical occurrence of metamorphosis and maturation demonstrated. Swarming at about 9 p.m. during a few hours. Epitocous forms allured by light.

8. NEREIS JAPONICA Izuka

(Annelida, Polychaeta).

Region of investigation Tojima Gulf, Inland Sea, Okayama prefecture, Japan; tidal range about 2 metres; investigator, Izuka (1908).

Just like *Ceratocephale osawai*, the immature form of the worm described by Izuka as *Nereis japonica*, lives between the tide marks, stays in its burrows during exposure and leaves its retirement, to creep about and feed, during the flood tide. A marked metamorphosis like in *Ceratocephale osawai*, does not occur in *Nereis japonica*.

Local fishermen, who use *Nereis japonica* as bait, or even as manure, in large quantities, appeared to possess the empirical knowledge, that swarming in this species is to be expected in the second half of December at spring tide, usually in one period, lasting a few days. "The period begins on the night just before the day of the new or full moon in the middle or the latter part of the month mentioned." Further the fishermen know "that it invariably takes place in the mid night just after the flood tide; and further that very rarely it occurs in two periods, close to the consecutive new and full moons." Izuka accompanied the fishermen in their boats, during their efforts to catch large quantities of the swarming worms, and observed that swarming commenced at December 15, 1906, reached its height at December 17/18, slowed down at December 19 and was absent on December 20, 1906, it being new moon at December 15. In the year 1907 large swarms appeared on December 20, at the day of full moon. Thus Izuka could corroborate the information given by the fishermen. Characterization: breeding period very short: second half of December; swarming maximum at new or full moon, seldom at new and full moon; swarming and nuptial dance in the middle of the night, just after the flood tide.

9. *SPIRORBIS BOREALIS* Daudin

(Annelida, Polychaeta).

Region of investigation Roscoff, Brittany, France; tidal range springs 7.2 metres, neaps 3.7 metres; investigator Garbarini (1933).

Repeatedly Garbarini collected at Concarneau (Brittany) and at Roscoff tufts of Fucus on which the spiral-shaped tubes of *Spirorbis borealis* were attached. In the laboratory of the marine biological station at Roscoff, he placed the Fucus in dishes and aquaria with sea-water, and he counted daily the number of larvae that was expelled from the maternal tubes. Spirorbis lays its eggs within the calcareous tubes, incubates the larvae during a short period, after which they escape at a given moment: "L'animal, hermaphrodite, pond ses oeufs dans son tube, ils y sont fécondés, et se développent en embryos, qui s'échappent à l'état de larves nageantes."

To his surprise Garbarini found, that emission of larvae showed clear-cut maxima at first and last quarters. These are the figures of some of his experiments:

STATION AND DATE	NUMBER OF LARVAE SET FREE								
	−3	−2	−1	Quarter	+1	+2	+3	+4	+5
Concarneau:									
24-8-1932, L.Q.	0	0	0	40	368	75	0	0	0
7-9-1932, F.Q.	26	100	110	48	40	0	0	0	0
23-9-1932, L.Q.	0	26	40	104	167	1172	198	0	0
Roscoff:									
6-10-1932, 11 petri-dishes	0	0	0	41	147	157	3	0	0
6-10-1932, aquarium No. 1	0	0	3	97	200	83	60	3	1
6-10-1932, aquarium No. 2	−	−	−	−	200	185	50	25	0
(First quarter)									

These results too fit in with the cases discussed. Probably egg-laying has its maxima at both of the spring tides, resulting in an emission of larvae roundabout both of the quarters.

Characterization: active breeding observed in August and September; sharp maxima in the emission of larvae at first and last quarter; maxima of egg-laying probably at or shortly after both of the spring tides; no data available about the exact time of the day the eggs are laid or the larvae are expelled.

10. *AMPHITRITE ORNATA* Verrill

(Annelida, Polychaeta).

Region of investigation Woods Hole, Massachusetts, on the Atlantic coast of the U.S.A.; tidal range spring tides 0.5 metres, neap tides 0.3 metres; investigator, Scott (1909).

Amphitrite ornata lives in mud tubes in the sea bottom about at the level of the low water mark at spring tide. Scott wanted eggs of Amphitrite in the course of one of the many sets of experiments on embryological development carried out in the Woods Hole Marine Laboratory in the beginning of this century. Incidentaly he found out, that it was not easy to procure mature eggs at any time in the summer season, but that "the egg laying reflex is closely associated with the time of spring tide, the height of the season occurring at the time of new or full moon or within two days after these dates."

The data collected by Scott on the rhythm in egg-laying in *Amphitrite ornata* are not very extensive and require further amplification before they suffice to convince us that a rhythm really exists.

Though Scott thinks of influences exercised by temperature and feeding conditions, and assumes that "the influence of the tides or the moon is entirely secondary," I am inclined to presume that, if the rhythm in Amphitrate's egg-laying really shows exact peaks at new and full moon, the same argumentation could be used as in the foregoing cases, to demonstrate that it is the tidal phenomenon which performs the trick.

Provisionally we can characterize this case as follows: breeding season June, July, August; maxima in egg-laying probably at new and full moon; no data available about the time of the day or the stage of the tide at which oviposition takes place.

CASES OF PERIODICITY IN BREEDING SHOWING A MARKED CORRELATION WITH THE TIDAL SEQUENCE

The ten cases discussed above are all remarkably similar:

A breeding period varying from several months to two weeks (No. 8, *Nereis japonica*).

A tidal range of quite a considerable magnitude, usually of more than 1 metre, this with the exception of that in Woods Hole (No. 10, *Amphitrite ornata*).

Maxima in swarming or egg-laying at complementary phases of the moon, either at new and full moon, at first and last quarter, or at a fixed number of days after new and full moon.

The close correlation between the rhythm in reproductive activities and the sequence of neaps and springs can be understood by assuming, that rhythmical variation in water pressure evokes a rhythmical maturation of the eggs.

Maturation is accomplished in a limited period, showing its final phase simultaneously in all individuals in the course of a few days, in extreme cases at one particular day. Then egg-laying or swarming occurs, often under well-defined conditions of light or tide. In many cases the mature animals wait till sunset or dusk before they proceed to perform their ceremonies. The mature animals often appeared to be very sensitive to relatively low intensities of illumination.

Rhythmical and simultaneous egg-ripening, and after that swarming or spawning at a definite hour of the day or at a definite stage of the tide, results in a marked concentration of breeding activity, which greatly enhances the chances of fertilization of the eggs and of a successful cross-breeding, thus being of paramount biological importance.

During my search in literature I came across two cases which at first sight cannot be ranked in the foregoing list. I shall explain below, why I am inclined to believe that they do belong in it, though I confess that further investigations are required to prove whether I am right or not in this assumption.

11. MYTILUS EDULIS L., MACOMA BALTHICA L., MYA ARENARIA L.

(Mollusca, Lamellibranchiata).

Region of investigation Passamaquoddy Bay, N. B., on the Atlantic coast of Canada; tidal range springs 8.0 metres, neaps 5.0 metres; investigator Battle (1932 a, b); observations in the year 1931.

Battle's investigation on rhythmical spawning in *Enchelyopus cimbrius* (Battle 1930, No. 3 of this list) led her to plotting a new set of observations in which both the production of eggs and the condition of the parental gonads could be checked. To this aim she choose the lamellibranch species *Mytilus edulis, Macoma balthica,* and *Mya arenaria,* which live in great numbers on the tidal flats in the stations St. Croix and Birch Cove in Passamaquoddy Bay. Battle checked the conditions of the gonads in samples of 100 to 150 specimens every 3 to 4 days during the season of reproduction, and managed moreover to check the number of larvae of *Mytilus edulis* in the plankton.

Battle came to the conclusion that the large majority of the animals of all three species mentioned, is inclined to breed simultaneously, and moreover in all three species "a close correspondance between the maturing and spawning of the ovary and testis" could be demonstrated. In Mytilus, Mya, and Macoma maxima in spawning were reached roundabout full moon, while spawning slowed down markedly at new moon. Data on the occurrence of larvae of *Mytilus edulis* fitted in remarkably well with a maximum in spawning at full moon (Fig. 4). Battle did her utmost to explain this phenomenon, but did not find

a plausible explanation. The mud flats on or in which the animals lived, were exposed at low tide, but no differences were detected between stations with 2 to 3, 3½ to 4½, and 5 to 5½ hours of exposure. Water temperature was remarkably equable during the period of her observations and certainly did not show peaks at well-defined phases of the moon. She concluded: "there does not seem to be a marked correlation between either air or water temperature and spawning." Still, Battle hoped to associate the phenomenon with temperature conditions and mentions the fact that during fine weather "at the neaps the temperature of the mud flats is raised during the mid-day exposure periods." She forgot to mention, however, that this certainly holds good for both first quarter and last quarter neaps, so that we do not agree with her when she assumes that: "this heating in the first quarter neaps may initiate spawning." Besides, she found that the time of exposure appeared to be without influence on the phenomenon of simultaneous spawning, and we can add, that an influence of temperature exercised during the periods of exposure, is not very plausible, for lamellibranches are in a state of rest or even anaesthesia during exposure.

All these considerations demonstrate that it is most improbable, that temperature conditions call forth the marked periodicity in spawning detected by Battle.

A closer study of Battle's diagrams reveals the remarkable fact, that in the region concerned great differences occur between full moon and new moon spring tides. In the year 1931, new moon spring tides reached a height of about 8 metres, and full moon spring tides were nearly obliterated, so that they hardly differed in amplitude from the neaps. In Figure 4 I reproduce Battle's diagram on *Mytilus edulis,* taking occasion to depict her data on the number of small mussel larvae in the same diagram. For the sake of uniformity I adopt her nomenclature in calling "tidal amplitude the difference in level between successive tides, either low and high or high and low."

Studying the course of tidal amplitudes we have to admit that this is a clear-cut case of a real spring tide (at new moon) next to an obliterated spring tide (at full moon) and therefore we should not be surprised to find rhythmical spawning in mollusks with only one peak during the lunar cycle. Therefore I assume that Battle's case should be ranked in the foregoing list of ten cases. Maturation of the eggs is initiated by the maximum in tidal amplitude at new moon, and spawning takes place about a fortnight later on.

Battle, in depicting her diagram, certainly has seen the enormous difference between new moon and full moon spring tides, but she did not dare to mention this in connection with the spawning activities, as she still clung to the old-fashioned idea that temperature is all-powerful in reproductive activities.

Battle made a simultaneous study of breeding activities in *Yoldia sapotilla* (Gould) living at a depth
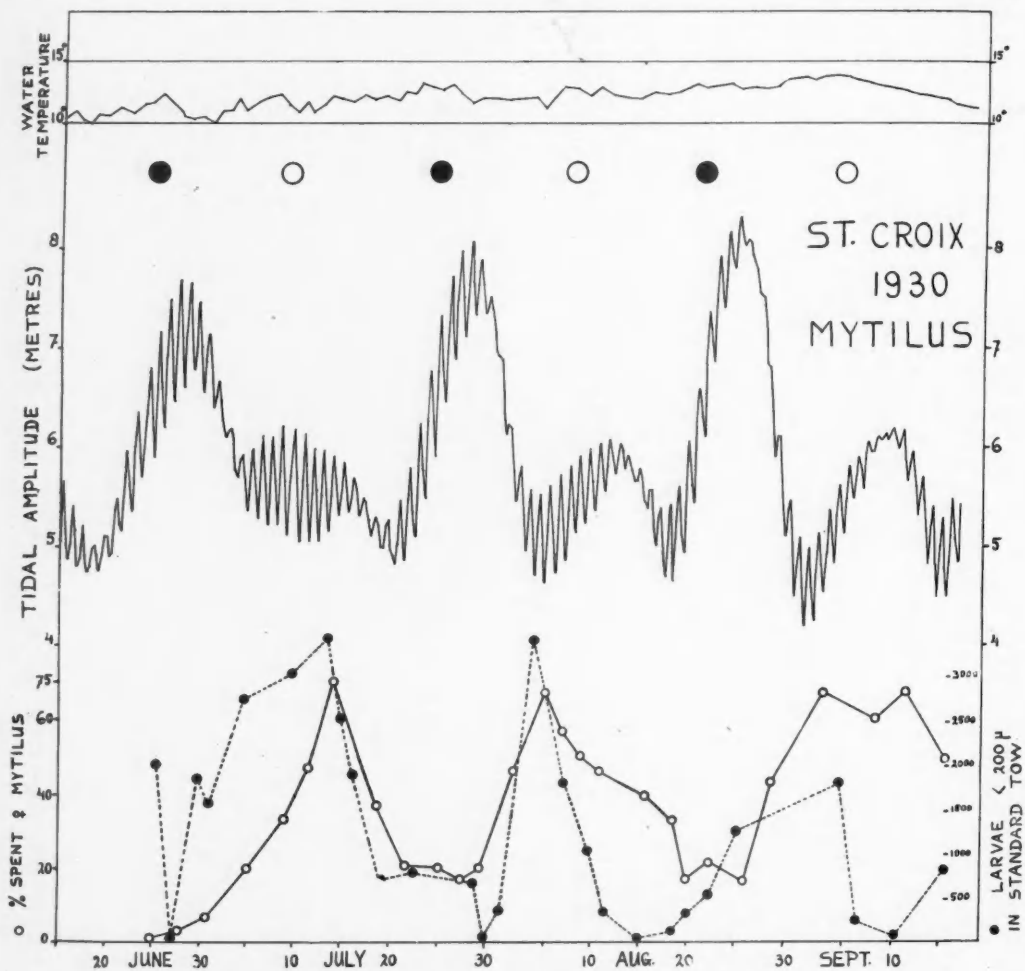
FIG. 4. Battle's data on reproduction in *Mytilus edulis* in Passamaquoddy Bay.

of about 20 to 30 metres and she found out, that this species shows a less regular rhythm in breeding, but her data are not sufficient to justify her conclusion, that Yorldia shows two maxima in breeding during the lunar cycle.

In discussing her data on Yoldia she mentions, though not without hesitation, that "it is possible that the increased hydrostatic pressure at the spring tides may initiate a greater degree of spawning at such times." Curiously enough she never mentions the differences in water pressure in connection with breeding activities in Mytilus, Mya, and Macoma.

One could ask why the fish *Enchelyopus cimbrius* studied by Battle in the same area in the years 1927 and 1928 did show two maxima in one lunar cycle. The answer is, that the differences between full moon spring tide and new moon spring tide were negligible in the years 1927 and 1928 and reached a maximum in the year 1931. The predomination of the new

moon spring tides alternates after a couple of years with the predomination of full moon spring tides, in the interjacent periods, the differences are smaller or even negligible. This in connection with the 9-years cycle of the moon's parallactic differences.

It would be most interesting if someone would care to repeat Battle's investigations in the same area in a year in which full moon spring tides are predominant and new moon springs obliterated. If my conception is right, Mytilus, Mya and Macoma should show maxima in spawning roundabout new moon then.

In a separate paper Battle (1932a) again discusses the data collected on breeding in *Mytilus edulis* and concludes, that the mussels should be eaten at new moon, a large percentage being spent roundabout full moon. In the light of the foregoing we can state that the year 1931 showed maxima in spawning at full moon, but that it is not improbable

that maxima in spawning will be found to occur at new moon in years in which the full moon spring tides predominate, and the new moon spring tides are obliterated. Moreover I can add, that we in Europe do not like to eat mussels in the season of reproduction and that mussels full of eggs or sperm are not to our taste. We prefer to wait till the spawning season is over and the mussels have developed a "new fish." I understand, however, that one cannot easily follow our methods in Canada with its short summer seasons and its long ice-bound winters.

We can characterize Battle's data on Mytilus, Mya, and Macoma concisely as follows: Breeding season during several months in summer. In the year 1931 marked maxima in spawning roundabout full moon, probably called forth by the initiation of maturation by the new moon spring tides, which predominated, while full moon spring tides were almost obliterated. Further investigations are required to prove, whether or not the reverse will be the case in a year in which full moon spring tides predominate.

12. POCILLOPHORA BULBOSA

(Coelenterata, Anthozoa)

Region of investigation Great Barrier Reef, N.E.-coast of Australia; tidal range spring tides 2.0 metres, neap tides 1.4 metres; investigators Marshall & Stephenson (1933).

A second case of masked tidal periodicity in reproduction has been revealed by Marshall & Stephenson during the Great Barrier Reef Expedition of 1928-29, in their efforts to establish "whether in a tropical marine area the breeding of common animals goes on fairly steadily all the year round, or whether there is a concerted season for the majority of these at some particular time of the year."

Their data concerning reproduction of the coral Pocillophora bulbosa are very interesting indeed. They collected a great number of samples by breaking off little branches from a number of colonies. In the laboratory the planulae, present on the branches, were counted. Though sampling was carried out quite frequently, many samples showed no planulae at all. Planulae were obtained at about the time of new moon in the months December, February, March and April (no sampling took place roundabout the January new moon), while planulae could not be detected in the many samples collected in the interjacent periods. Curiously enough, planulae were obtained at about the time of full moon in the months July and August, likewise showing zero values in interjacent periods. A transitional period could be demonstrated between the last of the new moon breeding periods (April) and the first of the full moon maxima (about July 20): "breeding occurred at and for some time after new moon in May and before full moon in June. During the interval between these two periods it died down less completely than usual, but the definite breeding period in June was delayed almost until full moon." Alas, no data are available for the second transitional

period, which should be placed between August and December.

"Is there any explanation which will help to elucidate a transition of this nature?" is the question put by the investigators. "So far as we can see at present there is none. There is a coincidence between the occurrence in question and the state of the tide, since during the summer months the lowest ebbs occur at the time of full moon and at night, whereas during the winter (May to October) they occur at the time of new moon and in day time; but whether there is any connection between the tidal cycle and the reproductive cycle of the coral it is impossible to tell."

It is comprehensable that the authors hesitated to ascribe the phenomenon observed to tidal features, as no clear-cut case of correlation between the sequence of neaps and springs and reproductive cycles had been demonstrated so far. Moreover, this case certainly is far too complicated, to be used as a solid foundation for the erection of the theory of tidal periodicity in reproduction.

In Figure 5 I depicted the variation in tidal amplitude in the station at Sydney and for the sake of uniformity I used Battle's nomenclature here too. I did not have at my disposal detailed tidal figures for the exact station at which the observations were carried out, but I found indications that the differences there will be rather more than less conspicuous than at Sydney. We see, that the full moon spring tides predominate during summer (December-March) and the new moon springs in winter in the particular year, which is in accordance with Marshall & Stephenson's information. Probably maturation is initiated by the predominating spring tides, resulting in a production of planulae about a fortnight later on, thus showing maxima in planulae at about the time of new moon in summer (December-March) and at about the time of full moon in winter (July, August), with a transitional period in between.

Curiously enough, the coral concerned seems to show a certain sluggishness in following the reversal of tidal predominancies, for even in April a new moon maximum in the occurrence of planulae was demonstrated, and one had to wait till July 20th before one found a clear-cut full moon maximum. Such a tenacity towards a once established rhythm is often observed in biology.

In this case of Pocillophora bulbosa too, we should like to possess data on periodicity in reproduction in a year with predominancy of full moon spring tides in the period June-September and of new moon spring tides from November till February, with a great many samples collected during both of the transitional periods. I am afraid, however, that it will be less easy to collect so many samples at the Great Barrier Reef than to check anew the breeding of the lamellibranchs in Passamaquoddy Bay.

Characterization: breeding period probably all the year round (no data available concerning the period September-November). In the period 1928-29 clear-cut maxima in planulae production at new moon from December to April and at full moon in July and
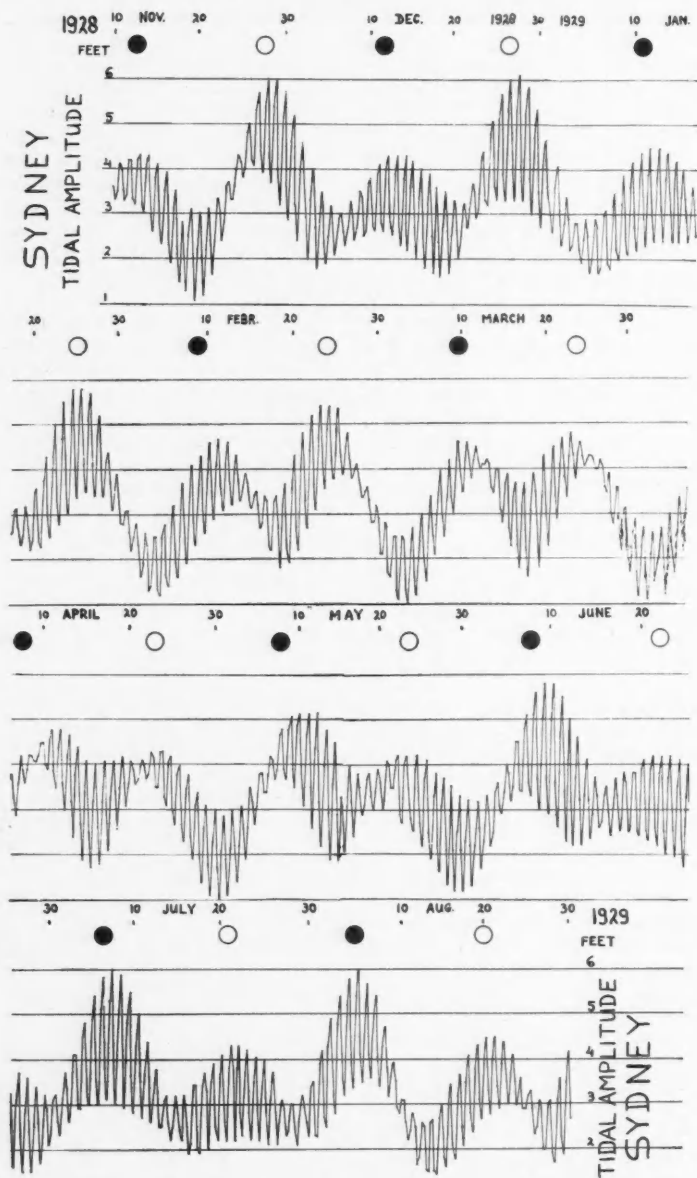
Fig. 5. Tidal amplitude at Sydney, 1928-29.

August, with a transition period in between. Probably this phenomenon should be associated with a predominancy of full moon spring tides in the period November-March, and of new moon spring tides from June to August in the year concerned.

MARINE ANIMALS SHOWING MAXIMA IN REPRODUCTION ONCE IN THE COURSE OF THE LUNAR CYCLE

The business of our science is to find uniformities in nature, and we should be pleased, if every case of lunar periodicity in reproduction appeared to fit in the theory discussed. This is, however, not the case. There are a number of animals, which show maxima in reproductive activities once in the course of the lunar cycle. The explanation used, pointing at a predominancy of one of the spring tides, does not hold good in these cases, as the tidal amplitude is quite insignificant in the areas concerned and as the maxima stick to the same phase of the moon (often situated between full moon and last quarter) in the different years, irrespective of slight predominancies of full or new moon spring tides.

The most spectacular case is that of the famous

Palolo-worm *(Eunice viridis)*, but to gain a better knowledge and insight in these phenomena I have chosen to consider Ranzi's extensive data on reproduction in *Platynereis dumerilii* near Naples. With the aid of these data, I shall try to construct a solid basis for similar cases, which will be treated separately below.

1. *PLATYNEREIS DUMERILII* Aud. & M. Edw.

(Annelida, Polychaeta).

Region of investigation Harbor of Mergellina, Naples, Italy; tidal range springs 0.45 metres, neaps 0.15 metres; investigator Ranzi (1931, 1931a): observations in 1929 and 1930.

Intrigued by the discrepancy in the results of several investigations on periodicity in reproduction, Ranzi plotted a set of observations to check periodicity in reproduction of swarming polychaetes in the Mediterranean. I consider his observations to be of particular value, for he combined a high frequency of sampling, carried through with great assiduity during an entire year, with the utmost caution in checking the reliability of his figures.

Ranzi chose the little harbor of Mergellina as his field of operations. In this harbor, which has a depth of 2 to 3 metres, he established 4 stations and at each of those Ranzi sampled during a fixed number of minutes, starting one hour after sunset, and this every day during the first three months, thereafter thrice a week. His samples cover the period of June 1929 to June 1930. Ranzi caught several species of polychaetes, but the species *Platynereis dumerilii* prevailed in his samples.

Ranzi used a lamp to allure the worms, and tried to catch them quantitatively during the fixed periods he placed his lamp in the water. In case the numbers of animals appearing in the lamps' radiation were not too large, Ranzi is quite sure to have caught them all, but if they came in enormous numbers, Ranzi's figures are probably on the lower side, as he probably missed some, so that his figures are certainly not exaggerated.

Ranzi found out, that the mature form of Platynereis, the so-called heteronereis, performing its nuptial dances at night in the surface layers of the water, is quite sensitive to differences in illumination. Therefore it was necessary, in order to collect comparable data, to stick to the same type of lamp, as a lamp of 150 candle power appeared to allure far less individuals than a lamp of 200 candle power. To investigate whether or not the number of worms swimming in the surface layers remained the same during the entire night, Ranzi sampled nine times during an entire night in the months June, July and August. The figures for the periods 21-22 h., 24-1 h. and 3-4 h. resemble each other very much, so that Ranzi is correct in stating : "Da questi dati sono autorizzato a concludere che la quantità di Heteronerei dumerilii attratta dalla lampada resta constante durante tutta la notte." Moreover his laboratory experiments showed him, that no variation in the intensity of phototactical attraction can be ob-

served in the course of the night: "D'altra parte nessuna differenza sensibila si osserva nelle diverse ore del giorno e della notte nel fototattismo delle Heteronereis tenuta in acquario in camera oscura."

Thus Ranzi found it possible to collect quantitative samples by placing his lamp in the water for periods of only 15 minutes in each of his 4 stations, starting one hour after sunset.

External conditions appeared to have little influence on the number of worms collected by Ranzi. Rain prevented the worms, from reaching the upper layers of the water and, this fact could easily be corroborated by laboratory experiments.: "Cominciai col notare che i giorni che aveva piovuto la cattura della Heteronereis era nulla o scarsissima," but fortunately rain, seldom disturbed Ranzi's observations. Currents and tides, being practically absent in this part of the Mediterranean, had no perceptible influence on the number of heteronerei collected by Ranzi. Moreover he soon found out, that the same number of worms could be caught before and after moonrise, and that an overcast sky did not prevent the worms from coming: "La luce lunare non sembra invece avere alcun effetto sulla quantità di Heteronerei attratta della lampada. Pescando in fatti prima e dopo il sorgere della luna, si ottiene lo steso risultato."

Ranzi's extensive data show that swarming of *Platynereis dumerilii* is of little or no importance in mid-winter, but from March to October inclusive Ranzi caught quite considerable numbers of them, swarming showing its height in July and August. So the breeding season appeared to be quite long.

In that breeding season Platynereis showed a marked periodicity. High numbers were collected roundabout full moon, the maximum showing its peak on an average, the 3rd day after full moon (exactly on this 3rd day in July, August, October, 1929; February, March, May, June, 1930), and minima, though seldom as low as zero, were demonstrated to occur at new moon and first quarter. In Figure 4 (upper part) I depicted the data collected by Ranzi in the year 1929. As his data for the months March to June, 1930 show exactly the same course, I did not judge it necessary to reproduce these too!

Ranzi did his best to explain this remarkable rhythm in the reproduction of *Platynereis dumerilii*. As the phenomenon has virtually the same character from March to October inclusive, which is expressed by Ranzi as follows: "si osserva scarsissima nei giorni che precedono la luna piena, aumente rapidamente con la luna piena, raggiunge un massimo il terzo giorno dopo la luna piena e decresce poi lentamente per raggiungere il minimo al primo quarto," it is no use to try to correlate it with temperature conditions. Temperature may be the cause of the slowing down of reproductive activity in winter and of the occurrence of very high figures in July and August, it cannot be held responsible for evoking the curious periodicity. Currents and tidal differences, being of very little importance here and showing about the same values twice in the lunar cycle, cannot be held responsible

either. To quote Ranzi: "Comprendere come una così piccola variazione di livello possa agire su animali che vivono a qualche metro di profondià, non so." Of course he tried to correlate the phenomenon directly with the moonlight, but as he could find no difference in swarming before and after moonrise, and as overcast skies gave the same results as bright weather, he found it quite a difficult task. Where moonlight is nothing but a little bit of reflected sunlight, Ranzi could not imagine what kind of influence moonlight could exercise on these worms, and at last, in his despair, he is inclined to believe in some kind of mysterious radiation, not noticed by us, so far: "pensare a qualche azione di nature ignota, tale da non essere percepita dai nostri mezzi di indagine, ma da essere percepita dagli organismi."

We need not take this desperate step, however, to find a plausible explanation! I believe, that Ranzi was quite "hot" when he remarked: "supposto che la luna agisca in una maniera qualunque nel determinare il differenziamento sessuali delle Platynereis" and "dopo un certo numero di giorni, dall' azione ambientale subordinata al ciclo lunare, cominciano le Platynereis a divenire Heteronereis e raggiungono questo stadio in forte quantità nei giorni che seguno la luna piena, mentre altre divengono Heteronerei solo nei giorni successive."

In my idea this is certainly the case. A maximum in swarming during a period of a few days, reaching its height the 3rd day after full moon, and independent of lesser variations in temperature, tides or light on these particular days, should be understood as the result of a rhythmical maturation of the animals. Tidal differences being nearly negligible here, and the phenomenon occurring only once in the lunar cycle, we wonder what factor sees to a rhythmical ripening of the gonads here.

When we consider that Platynereis can be found sheltered under seaweed or stones during the day and leaves its burrows only during the night in search of food, and when we know, that this animal possesses four well-developed eyes, we come to the conclusion, that it will not be indifferent to these creatures whether the night is dark or moonlit. Hiding in its dark shelter during the daylight hours, this rhythm of the moon must be of utmost importance to this and kindred marine animals living in shallow places. We know that birds react sharply to rhythmical differences in illumination (the lengthening and shortening of the days) in their sexual activities, and that many plants are highly sensitive to the length of the day (so more to the number of hours of illumination than to the intensity of the light) in their breeding activities. Could it surprise us, if the rhythmical alternation of dark nights and moonlit nights exercised some influence on sexual maturation in nocturnal animals living in shallow water?

This is how I see it. The animals are only active during the night, and in the breeding season the period of moonlit nights (the waxing of the moon) initiates sexual ripening, resulting in swarming during a short, well-defined period of the lunar cycle.

This is the only plausible explanation for the phenomenon observed by Ranzi and we shall see, that more sets of observation on other species of animals with nocturnal habits, fit in remarkable well with this hypothesis.

Ranzi's data are so reliable and extensive, that we need not bother about discrepancies of his data with those of several other observations on Platynereis dumerilii.

Hempelmann (1911) collected incidentally a number of heteronerei of Platynereis dumerilii at Naples in plankton samples procured at sunrise, but his figures are far too small to base conclusions on.

Gravier & Dantan (1928) collected an extensive material in the often wind swept Bay of Alger (French North Africa) with the aid of a lamp. Platynereis dumerilii was found to be present in several of their samples, but did not show a very exact rhythm in its occurrence. In fact, only once did they catch large quantities of this worm, i.e. on 24-9-1926 and that was 3 days after full moon, so in accordance with Ranzi's data!

Georgévitch (1938) fished with a lamp near Split (Dalmatia, Yugoslavia) and caught Platynereis dumerilii too, but something must be wrong in his description: "À la mer tranquille les polychètes se rassemblent sous la lampe au temps du premier et du dernier quart de la lune, pendant l'obscurité, et alors seulement pendant les premières heures de la nuit, avant la sortie de la lune." The latter is only possible at the last quarter and I am inclined to believe that he caught his worms roundabout that quarter and that the first quarter only slipped in accidentally, probably under the influence of Hempelmann (1911).

The data collected by Fage & Legendre, which have been discussed more amply, and depicted in Figure 4, ought to be considered as quite reliable, however. We could think of geographical races of Platynereis dumerilii, each having a special kind of rhythm in its reproduction, but I do not believe that it is necessary to assume this. Ranzi is of the same opinion: "Per spiegare una simile sconcordanza invocara razze locali mi sembra difficile." I believe that Platynereis dumerilii's sexual maturation can be influenced by both a rhythmical variation in water pressure (sequence of neaps and springs) and a rhythmical alternation of periods of dark and moonlit nights (cf. the discussion of Eunice fucata which follows). In case the tidal range is considerable (several metres in Brittany), the tidal influence predominates, but in case the tidal phenomenon is negligible, like in the Mediterranean, moonlight is inclined to preponderate.

We should not be surprised to find that more species of marine invertebrates with nocturnal habits, provided with well-developed eyes and living in shallow water, performed the same rhythm in reproduction as Platynereis dumerilii at Naples. As a rule this will be the case in regions where the tidal differences are small or even negligible and especially in animals, which live permanently in water, for animals

living on the tidal flats often are not strictly noc-turnal, and often creep about in search of food dur-ing the few hours of high water, irrespective of night and day.

We can characterize Platynereis' behavior at Naples concisely as follows: Breeding season from March to October inclusive, showing its height in July and August. Maxima in reproduction, probably corre-lated with nocturnal habits and the sequence of dark and moonlit periods, shortly after full moon, show-ing its highest peaks three days after full moon. Swarming in the surface layers in all the hours of the night, except in rainy weather.

2. *PLATYNEREIS* SP.

(Annelida, Polychaeta).

Region of investigation harbor of Madras, India; tidal range springs 0.95 metres, neaps 0.55 metres; investigators, Aiyar & Panikkar (1937).

Inside the Madras harbor, the authors observed swarming of *Platynereis* sp. on March 22, 1936 in the first hours of the night at new moon. This led to regular observations, in the first few weeks daily, but as swarming appeared to stay away, Aiyar & Panikkar soon confined themselves to make observa-tions in the Madras harbor roundabout full and new moon only. The next time swarming occurred was from 18 to 20 June, 1936, with a maximum on the 19th, it being new moon on the 18th. The third and last time they witnessed this phenomenon was on September 15, 1936, one day before new moon. The authors are quite sure that no swarming took place roundabout full moon. They carried on with their observations till March, 1937, but never saw swarm-ing again.

Though the data are quite scanty in this case and amplification should be very welcome, I should like to rank this species provisionally in the list of ani-mals showing maxima once in the lunar cycle. The tidal range is of little importance here and water temperature is quite equable throughout the year. If we compare this case with *Platynereis dumerilii* at Naples, we see that swarming comes far later at Madras, but we are not obliged to assume that every species requires the same number of days for matura-tion and that the initiation of egg-ripening associated with the waxing moon starts at the very same stage in different species. Further we found maxima every month at Naples, though often of a different magni-tude, while intervals of 3 month duration were dem-onstrated twice at Madras. This does not mean, however, that the worms at Naples produce eggs every month, and those at Madras every 3 months, for in fact the different maxima are brought about by different individuals, as Platynereis dies most prob-ably after performance of its nuptial dance.

Characterization: breeding observed in March, June and September 1936; maxima in swarming only observed at new moon, possibly associated with the moon's cycle. Swarming between 7 and 10 p.m.

3. *PLATYNEREIS MEGALOPS*

(Annelida, Polychaeta).

Region of investigation Woods Hole, Massachu-setts, on the Atlantic coast of the U.S.A.; tidal range springs 0.5 metres, neaps 0.3 metres, investigator, Just (1914).

In the Woods Hole area *Platynereis megalops* may appear in numbers in the upper layers of the sea, to perform its nuptial dances. Just tried to collect data concerning a possible periodicity in this swarming and carried through observations in the years 1911, 1912 and 1913. Especially in the year 1913 he often "went out every night, giving attention wholly to Platynereis' swarming." Despite of this high frequency sampling Just witnessed but once a very spectacular swarming, during which thousands of heteronerei were seen. Several times Just ob-served maxima of smaller importance, sometimes in several consecutive nights. He found his worms only in the first few hours of the night and none towards or at sunrise. Though apart from the dense swarm on August 11, 1912, his figures are quite modest, they suffice to conclude that *Platynereis megalops* swarms in the period between last quarter and new moon, showing diffuse maxima. Just never found the swarming worms between new and full moon. The great maxima of 11-8-1912 took place a few days before new moon.

More data are desired, but provisionally I prefer to characterize breeding activities in this species as follows: breeding observed in June, July and August. Diffuse maxima in swarming between last quarter and new moon, probably associated with the alterna-tion of dark periods with periods with moonlit nights. Swarming in the first few hours of the night.

4. *ODONTOSYLLIS ENOPLA* Verrill

(Annelida, Polychaeta).

Region of investigation Bermuda, Atlantic Ocean; tidal range springs 0.7 metres, neaps 0.3 metres; in-vestigators, Galloway & Welch (1911). Observa-tions in 1904.

Swarming in *Odontosyllis enopla* offers a very attractive spectacle as the luminosity of the females serves as an adequate lure for the males. The au-thors witnessed swarming in Harrington Sound, Bermuda, thrice in the year 1904: at 3-7 July (maxi-mum 4 July), at 29-31 July (maximum 30 July) and at 23 August (maximum of moderate impor-tance) in all three cases about at last quarter. The worms appear "within fifteen minutes of the same time, just as dusk was becomnig pronounced. The display only lasted for twenty to thirty minutes." The authors suggest that there is an annual, as well as a daily and monthly rhythm, and this fits in with our other cases.

Characterization: breeding period July, August (annual rhythm), maxima at last quarter (monthly rhythm), probably associated with the sequence of dark and moonlit nights (tidal amplitude insignifi-cant). Swarming shortly after sunset (daily rhythm).

5. ODONTOSYLLIS HYALINA Grube

(Annelida, Polychaeta).

Region of investigation Bay of Batavia, Java, East Indies; tidal range springs 1.1 metres, neaps 0.4 metres; investigator, van Lummel (1932).

Enormous numbers of small luminous worms were observed to swarm in the Bay of Batavia, in shallow places above the reefs, during the three nights following full moon. The worms appear shortly after sunset and are very sensitive to light, as could be demonstrated in vitro. A maximum in swarming was to be observed the second day after full moon: "op den tweeden dag na volle maan zijn zij zoo overvloedig aanwezig, dat het is, als ziet men een sterrenhemel in zee."

A metamorphosis during which long swimming bristles develop and the eyes increase in size, preceeds swarming. Van Lummel could observe swarming in *Odontosyllis hyalina* at full moon during all the months of the year: "Dit lichtfeest hebik het geheele jaar door, dus nu reeds 12 maal, gevolgd."

Characterization: breeding period all the year round. Maxima in swarming the first three days following full moon, probably evoked by rhythmical maturation in close correlation with the light of the waxing moon (nocturnal habits, sensitive to light, shallow places, tidal amplitude insignificant, maximum once during the lunar cycle). Swarming after sunset.

6. *ODONTOSYLLIS* SP.

(Annelida, Polychaeta).

Region of investigation Bahama Islands, Atlantic Ocean; tidal range springs 0.7 metres neaps 0.5 metres; investigator Crawshay (1935).

"While engaged on the sponge fishery investigations of the Colonial Office" Crawshay had the opportunity to witness swarming of a luminous Polychaet worm, a kind of Odontosyllis, several times. The phenomenon was always observed roundabout last quarter, 6 out of 7 times even within 24 hours of the last quarter. The time of appearance did not coincide with approaching dark, but often came later in the night. "The period of illumination is always very brief, usually not exceeding 5-10 minutes from first to last. It may perhaps be repeated on a following night, but more usually will not recurr until the same phase of a subsequent lunation." The phenomenon was actually observed in the months January, April, May, July, October and December. Crawshay gives a description of the luminous spectacle of this worm's nuptial dance, resembling very much a similar description to be found in the paper of Galloway & Welch.

Crawshay associates this swarming with the mysterious light seen from the poop of Columbus' vessel "Santa Maria" in this same region on 11-10-1492 (last quarter) at 10 p.m., for which so far no satisfactory explanation was given.

Characterization: breeding period all the year round. Maxima at last quarter, "wholly associated with the reproductive process," probably caused by simultaneous maturation associated with the periods of moonlit nights. Swarming within a few hours after sunset.

7. *EUNICE VIRIDIS* (Gray)

(Annelida, Polychaeta).

Region of investigation Samoa islands (Pacific Ocean), Levuka (Fiji islands, Pacific Ocean); tidal range springs 1.0 metres, neaps 0.60 metres; investigators Collin (1897), Corney (1922), Friedländer (1898, 1899, 1899a, 1901, 1904), Gravier (1924), Krämer (1899, 1899a), Woodworth (1903, 1907).

The natives of the Samoa and Fiji islands know since time immemorial that the Palolo worm can be expected to swarm above certain old coral reefs, often in incredible numbers, at the last quarter of October and November (Samoa) or of November and December (Fiji). As baked Palolo worms are one of their favorite dishes, swarming of the Palolo always calls for a gaudy feast. Missionaries reported about it, but it was only in the last few years of the 19th century, that one tried to reveal the real nature of this phenomenon. The swarming worms puzzled the investigators, for one could not detect a head! After a careful study they found out that the swarming worms were nothing but the posterior part of a polychaete worm of the genus Eunice, tightly filled with eggs (which give the worm a blueish green color) or sperm (giving the worm a red or brown color), while the anterior and thicker part of the animal, included its head, remained in its shelter in the old honey-combed coral rocks. The posterior or epitocous part of the body is far thinner and longer, than the anterior part and carries eye-spots at the ventral side of each of the numerous segments. The worms were detected in the old decaying coral rocks almost simultaneously by several investigators. It was Friedländer (1909), who procured the first worm that clearly displayed the transition from thicker anterior part to the thin epitocous part of the body, but the way he defended his priority in his papers (1904), is far from sympathetic: "dass der zoologische Hauptteil der Palolo-Frage von mir, und zwar von mir zuerst, und von mir allein, definitiv entschieden worden ist."

It is, however, the peculiar rhythm in swarming, which attracts our attention presently. So many data have been collected on the occurrence of the swarms of the Palolo-worm, that not the slightest doubt remains, that they appear at last quarter of the months mentioned, indeed. Corney (1922) gives a list of dates covering 25 years of observation at Levuka (Fiji), and as his paper is quite rare in our libraries, I reproduce herewith his tabulation in full, to show with how great a regularity the swarms appeared.:

1897	17	November	F.M.—8
1898	7	November	F.M.—9
1899	25	November	F.M.—8
1900	14	November	F.M.—8
1901	5	December	F.M.—9
1902	22	December	F.M.—7
1903	11	December	F.M.—7
1904	1	December	F.M.—9
1905	19	December	F.M.—8

1906	9	December	F.M.—9
1907	28	November	F.M.—9
1908	17	November	F.M.—9
1909	5	December	F.M.—8
1910	25	November	F.M.—8
1911	13	November	F.M.—7
1912	2–3	December	F.M.—8/9
1913	21	December	F.M.—8
1914	11	December	F.M.—8
1915	29–30	November	F.M.—8/9
1916	17	November	F.M.—8
1917	7	November	F.M.—8
1918	26	November	F.M.—8
1919	16	November	F.M.—8
1920	4	December	F.M.—9
1921	23	November	F.M.—8

Many are the efforts to give a plausible explanation of the sudden and regular appearance of dense swarms of the Palolo worm. The tidal rhythm is not very impressive in these Pacific waters and though slight differences between full moon and new moon spring tides may be observed, predominancy of full moon spring tides alternates with preponderation of new moon spring tides a couple of years later. As Eunice only appears at last quarter and stays away at first quarter, we can agree with Friedländer, that the tides cannot be held responsible ("zufolge die Gezeiten ist das Paloloproblem nicht zu erklären"). Woodworth statement "the Palolo makes its appearance in Samoa in the months of October and November during the last quarter of the moon. This is the time of lowest spring tides, when the reef flats in shallow places are uncovered or only awash, and at this season the sun is nearest to the zenith" is not quite correct, as last quarter coincides with neap tides and as spring tides occur twice during the lunar cycle. Perhaps Woodworth wants to give an explanation of the somewhat higher water temperatures in this time of the year, but this can only help us in finding an explanation for the occurrence of the breeding season in the months mentioned and not for the peculiar rhythm.

Krämer placed blocks of coral containing the worms in a pail filled with sea water the day preceding last quarter and saw that the worms swarmed in the pail (without tidal influence) as they did outside in the sea. Though the possibility remains that lack of oxygen in the pail of water forced the worms out of the stone, we should not be surprised to find the worm swarming under controlled oxygen conditions too, as the worm starts swarming after termination of the maturation process.

Friedländer tried to correlate the phenomenon with differences in illumination, but as he found that swarming took place in the early morning before dawn and that an overcast sky intercepting the moonlight did not prevent the worm's appearance, he did not succeed in finding a plausible explanation. In his despair he caught at Arrhenius' quaint, never corroborated theory, that the phases of the moon could exercise an influence on living beings, by causing differences in air-electricity, but after a careful study Friedländer admitted that he found himself forced to reject this possibility, and that the periodicity remained "volkommen rätselhaft."

Friedländer could have devised a plausible explanation but for his lack of biological imagination. He suggests once the possibility that maturation could initiate at the full moon spring tide, but later on he did not mention it again. He cannot see how on earth the moon can exercise an influence on the adult worm living coiled up in its burrow in the coral rocks.

Krämer (1899) had a better idea of the animals way of living: "Nun liebt aber der Palolo das Licht nicht; sein Freund ist die dunkele Nacht, wenn er auf Abenteuer ausgeht." Here is the key to the problem! The Palolo worm living in shallow water (but not in the tidal lands) is to be found coiled up in a burrow in the old honey-combed coral rocks during the daylight hours. It cannot stay there forever, for it has to collect its food. Being no plankton-strainer or rock-eater, it finds itself obliged to leave its burrow, at least with its anterior part, which it does during the hours of the night. Krämer is certainly right in stating that the Palolo has a nocturnal style of living. The tides being of little importance and temperature being quite equable throughout the year, at most showing a slight increase during spring and summer (October, November, December), the rhythmical sequence of periods with dark and moonlit nights must be of paramount importance in this animals biology. During the breeding season, which is quite short in this worm, the moonlit nights evoke a simultaneous ripening of the gonads. It is not the intensity of moonlight that counts most—this being somewhat different at various depths—but the number of hours of nocturnal illumination, analogous to maturation in birds and plants. At full moon the maturation process is in full swing and at last quarter all the worms reach maturity about at the same day. Then they proceed, at a particular phase of the tide to cast off the posterior epitocous part, which immediately starts to swim towards the surface. At one particular night swarming reaches its height, the nights before and after show the predecessors and late comers. Swarming is executed at low tide, in the dark of the night, irrespective of lunar illumination conditions.

I believe that this is the whole secret, an explanation far simpler than the invocation of aid from the side of air-electricity or polarized moonrays, and moreover in accordance with the events in many other nocturnal, but light-sensitive animals.

We can characterize *Eunice viridis'* behavior concisely as follows: Breeding season at Samoa (13°41′ S.) October, November, seldom December, at Fiji (17°41′ S. and getting its spring about a fortnight later than Samoa) November, December, seldom January. New Hebrids (Gravier 1924) October. Clear-cut swarming maxima roundabout last quarter, most probably brought about by rhythmical maturation closely correlated with the sequence of periods of dark and moonlit nights. Nocturnal habits. Epitocous part very sensitive to light, swarms in tight masses in the surface layers of the sea. Swarming at Upolu (Samoa) shortly before sunrise at low

water, at Tutuila island (Samoa) about at midnight, at the New Hebrides from 9 till 11 p.m.: "le soir du dernier quartier de la lune qui commence en Octobre. Les vers se montrent vers 9 heures du soir et vers 11 heures ils disparurent pour ne plus revenir que l'année suivante à la même époque."

Though it remains a remarkable fact, that *Eunice viridis* shows quite a short breeding season in this tropical region with its quite equable temperatures),[2] and that egg-ripening progresses so neatly simultaneous in all the individuals of the colony, and though experimental evidence on the influence of moonlight on maturation would be most welcome indeed, I believe, that my theory is quite a simple and plausible one, thus removing much of the Palolo mystery.

8. *EUNICE FUCTATA* Ehlers

(Annelida, Polychaeta).

Region of investigation Tortugas Islands, Florida, U.S.A.; tidal range springs 0.5 metres, neaps 0.2 metres; investigators, Mayer (1900, 1902, 1908), Treadwell (1909, 1914), Clark (1937, 1938).

Remarkably conformable to the Palolo worm's habits proved to be the swarming behavior of its near relative *Eunice fucata*, detected by Mayer (1900). This worm, with good reason called the Atlantic Palolo, appeared to swarm in dense masses above the old decayed coral reefs near Tortugas Islands on July 9, 1898 (last quarter −1) and on July 1, 1899 (last quarter +2), and that at the time of sunrise. Mayer looked out for swarming at other dates, but though he sailed early every morning from June 25, 1898 to August 19, 1898 and from May 17, 1899 to July 4, 1899, he only witnessed dense swarming at the days mentioned, and slight swarming on the days immediately preceding or succeeding these maxima.

Mayer had the opportunity to carry out further investigations, and soon he found out, that conditions resembled very much those described for *Eunice viridis*. Here too the worms appeared to live in great number in shallow parts of the sea, below the low water level, within "crevices in dead corroded coral or in limestone beach rock, which has been honey-combed by the burrows of marine animals" (Mayer 1908). During the daytime he found that "the animal lies coiled upon itself within this burrow" (Mayer 1902). In the breeding period (June, July) metamorphosis takes place in the adult worms, during which a posterior epitocous part of the body, tightly filled with eggs or sperm, is developed. Swarming appeared to take place "within three days of the day of last quarter of the moon between June 29 and July 28" (Mayer 1908). "Before sunrise on the morning of the day of the annual breeding swarm the worm crawls out backwards from its burrow, until all of the sexual segments and a portion of the slender middle part of its body have

been protruded. A vigorous helical, corkscrew-like twisting movement then comes over the sexual segments" (Mayer 1908). Finally the epitocous part snaps off at the junction between the two parts of the body and darts to the surface, swimming tail-end first. Mayer was in a position to witness the breaking away of the epitocous part, as mature worms disturbed by breaking open their burrows, are inclined to perform this behavior at any time of the day, which could be called "abortive swarming."

Natural swarming "commenced very early in the morning, before sunrise, and soon vast numbers of the worm were to be seen swimming upon the surface of the ocean." (Mayer 1900). They had "no tendency to congregate in masses, each worm pursuing its own course." Mayer (1908) added: "I have seen these in such abundance over the surface above the coral reefs at Tortugas, that hardly a square foot of the surface was free of a worm." At sunrise the swimming worms "begin to contract violently, so that the sexual products are cast out through rents and tears in the dermo-muscular wall." Mayer is certainly right in supposing that the swarming behavior greatly enhances fertilization possibilities.

Gradually more details were found out. In my eyes the most important one was Mayer's detection (1902) that "none of the eggs become mature until the time of the normal swarm, when all the eggs mature simultaneously." Artificial fertilization with living sperm added to eggs taken from animals collected in their burrow, proved to be impossible till 12 hours before the moment of natural spawning! So here too, it is simultaneous maturation which is closely correlated with the swarming phenomenon. Later Treadwell (1914) could corroborate that egg-maturation proceeded as the swarming date approached by demonstrating that the CO_2 output of eggs taken from the mother animal rapidly increased as ripening proceeded, which led him to the conclusion that "a definite increase in metabolism goes on in the egg as it approaches maturity," and that at least "some part of the stimulus leading to egg-laying comes from the activity of the egg itself."

Mayer carried out a series of experiments to establish which factor could be held responsible for causing the swarming phenomenon, and later Treadwell and Clark followed in his steps. Mayer placed pieces of rock containing living worms in spacious floating life-cars in which ample circulation was secured, while overheating during the warmer part of the day was efficiently counteracted. Moonlight was freely admitted and it appeared that in all three experiments, during which the worms stayed respectively thirty, four, and thirty days preceding natural swarming in the boxes, some of the worms swarmed normally within three days of the last quarter of the July moon. Mayer does not mention whether or not he saw to an appropriate feeding of his worms. "On the other hand, the worms never swarmed when the moonlight was prevented from falling upon the rocks within which they lived." This led Mayer to the assumption that moonlight

[2] Should we say with Ranzi (1931) "sol che allo stimulo lunare si associa un altra stimulo, probabilemente di natura interna, che permette la maturità solo in un breve periodo dell'anno," or should we think at the influence of the slightly higher summer temperature of the water, like in our oysters?

had an influence on his worms. He failed, however, in making a clear distinction between an influence on the maturation process and conditions required for the performance of the swarming phenomenon itself. This finally led him astray. Thus he tells us that in nature the worms will even swarm in overcast or cloudy weather, so that "even diffuse moonlight appears to be capable of calling forth the breeding swarm" and at the time of Treadwell's demonstration (1909) that the worm still swarms if the rocks containing them are placed in a dark chamber upon the day preceding the night of the swarming, Mayer thought that his supposition that the presence of moonlight is necessary for the swarming reaction, was severely shaken.

After the discussions on similar cases, we conclude that maturation in *Eunice fucata* is influenced by the occurrence of a series of moonlit nights in its breeding season. Simultaneous maturation advances and swarming takes place at the very day the eggs are ripe and here too at a special hour of the day (sunrise). Some worms attain maturity one or two days before, others somewhat later than the large majority, thus calling forth swarming of little importance on the days preceding or succeeding the big swarming maximum.

Moonlight is of no importance during swarming itself, and we can easily understand why the worms swarmed in overcast weather and in Treadwell's dark chamber.

Mayer supposes that *Eunice fucata* permanently stays in its burrow, coiled upon itself, but we feel sure that this animal too has noctural habits. Clark's observations (1937) give strong indication that our supposition is the right one, for he demonstrated that the immature worms are positive to light from 0.001 to 0.01 foot-candles and negative to higher illumination. The epitocous parts, swarming at sunrise, showed other figures: "swimming sexual ends are positive to intensities from 0.0005 foot-candles (the threshold) to at least 50 foot-candles and negative to gravity."

Still we cannot consider *Eunice fucata* to be a well-selected species in the carrying out of experiments to lay bare the roots of lunar periodicity, as its case is quite a complicated one. Mayer (1908) saw that the worms in the life-cars did not perform swarming 100%, as in nature, even if moonlight was freely admitted, as some worms "did not cast off their posterior ends, but remained passive in their burrows." Though we should admit that the number of worms used in his experiments is not overwhelmingly great, Mayer is probably right in assuming that "changing pressure due to rise and fall of the tide over the reefs is a contributory factor, but not a necessary component of the stimulus which calls forth the breeding swarm."

Observations on the occurrence of swarming in nature support this view. Though Clark (1938) showed that some eggs may be found floating in the water during many days of the breeding season and that swarming on a very small scale is easily overlooked, the occurrence of sharp maxima in swarming cannot be denied. Treadwell (1914) gives a list of swarming dates, in which the dates of principal swarming are printed in italics.

Year	Date	Phase of the moon
1898	July *9*, 10	L.Q. — 1
1899	July *1*, 2	L.Q. + 2
1900	July *19*	L.Q. + 1
1902	July *24*, *25*, 28	L.Q. — 2, 3
1903	July *17*	L.Q.
1905	July 9, 10, *21*, *22*, *23*, 24	L.Q. — 2
1906	July *11*, *12*, 13	L.Q. — 1, 2
1907	July *2*, *3*	L.Q. + 0, 1
1908	July *10*, 19	F.Q. + 4, L.Q.
1909	July 6, 7	L.Q. — 3, 4
1910	June *29*, *30*	L.Q.
1911	July *16*, 17	L.Q. — 1, 2
1912	July 6, 7	L.Q.
1914	July *11*	L.Q. — 3

The years 1905 and 1908 showed swarming both at the first and at the last quarter. Apparently the moon is not all-powerful in this species, so Mayer is right in assuming that tidal influence is a component in calling forth swarming. Mayer said: "when the last quarter falls late in July, there may be a response to the first quarter as well as to the last quarter." Treadwell's table suggests, however, that the word "July" should be replaced by "breeding season," which does not necessarily stick very closely to our calendar. Without a doubt the influence of moonlit nights preponderate in this species, which lives in water with quite a modest tidal range.

However strange a simultaneous influence of two factors as different as moonlight and tidal sequence may seem at first sight, I should like to recall that *Platynereis dumerilii* proved to perform a rhythm correlated with the moon at Naples, where the tidal range is very small, and correlated with the sequence of neaps and springs at Concarneau, where the tidal range is considerable.

Characterization: breeding period very short: June 27-July 28. Swarming maxima within three days of the moon's last quarter; smaller swarming maxima may occur one or two days preceding or succeeding the day of the densest swarm. Swarming closely associated with egg-maturation. In mature animals the posterior epitocous part of the body twists itself loose and darts to the surface, where eggs or sperm are shed at sunrise. Maturation correlated with the period of moonlit nights, the worms living in shallow water and having nocturnal habits. Influence of the sequence of neaps and springs not entirely suppressed, but sometimes causing auxilliary swarming at first quarter.

9. *LYSIDICE OELE* Horst

(Annelida, Polychaeta).

Region of investigation Ambon, Moluccas, East Indies; tidal range springs 1.2 metres, neaps 1.0 metres; investigators, Rumphius (1705), Horst (1902).

Perhaps the earliest records on lunar periodicity are those noted down by Rumphius, who tells us

about swarming of a polychaete worm in the Ambon coastal waters, where it was collected by the native fishermen, who considered it as a delicacy. Rumphius tells us, that swarming could be expected in places where the immersed rocks are honey-combed, "waar groote rotsen in zee staan, die vol scheuren zijn." Swarming occurred on the 2nd, 3rd and 4th day after the February and March full moon. Rumphius, who spent most of his life as a naturalist on the island of Ambon, gives a number of dates on which swarming occurred (1684-1694), from which can be derived, that swarming really took place in the periods mentioned. Apparently it is quite a similar case as swarming in Pacific and Atlantic palolos.

Curiously enough, we are not yet sure about the systematic place of Rumpius' "wawo." Though Horst called this worm *Lysidice oele*, after specimen he found in a sample of worms said to be the "wawo," and presented by the assistant-resident of Banda to Max Weber, the leader of the Siboga expedition, there remains doubt. Fauvel found *Eunice viridis* in samples collected at Ambon, and zoologists witnessing the Palolo's swarming often describe swarming of smaller species of Polychaets, frequently belonging to the genus Lysidice. This happened in the days before or after the major swarming maximum of the Palolo.

It is possible that Rumphius' worm was nothing but *Eunice viridis* and that *Lysidice oele*, showing likewise lunar periodicity in swarming, was not the tasty species sought after by the Ambon fishermen.

Characterization: breeding period February, March. Maxima in swarming 2nd, 3rd and 4th day after full moon, most probably correlated with the occurrence of periods with moonlit nights. Swarming at sunset. Systematic position of the worm remains uncertain. Possibly *Lysidice oele* is only a species of minor importance, showing the same type of lunar periodicity.

10. *CHAETOPLEURA APICULATA* (Say)

(Mollusca, Amphineura).

Region of investigation Woods Hole, Massachusetts, on the Atlantic coast of U.S.A.; tidal range springs 0.5 metres, neaps 0.3 metres; investigator, Grave (1922).

Grave, in search of eggs of *Chaetopleura apiculata*, which he needed for embryological investigations, soon found out, that these were not always available in large quantities throughout the season of reproduction. On the contrary, periods of an ample egg-production alternated with periods during which it was difficult to procure ripe eggs. Checking of samples in the years 1919, 1920 and 1921 led him to the conclusion that "eggs may be had in small quantities at almost any time. By far the greatest spawning activity, however, comes at the approach of full moon and continues for ten days or two weeks." Spawning activity appeared to be of very little importance between new moon and a few days before full moon.

In the laboratory the eggs were laid between 7:30 p.m. and 10:30 p.m., but only during slack water, currents preventing the animals to spawn. Isolation of the individuals did not prevent them from spawning normally. No doubt Chaetopleura, being sensitive to light, like other Chitons, and showing nocturnal habits, is influenced in its process of maturation by periods of moonlit nights, resulting in diffuse maxima in spawning from full moon to the last quarter.

Grave's data are published in most unsurveyable protocols; tables and graphs are lacking and attempts to produce these with the aid of his heterogeneous protocols failed. Still I believe, that he is right in his main conclusion, and that *Chaetopleura apiculata* belongs to our list of animals influenced in its spawning by periods of moonlit nights, be it, that its periodicity in spawning does not reach that degree of perfection we witnessed in Eunice and several other species.

Characterization: breeding observed during the summer months. Diffuse maxima in spawning between full moon and last quarter, marked minima from new moon to a few days before full moon. Correlation with moonlit nights in this light-sensitive animal with nocturnal habits, probable. Spawning from 7:30 p.m. to 10:30 p.m. at slack water.

11. *ACANTHOZOSTERA GEMMATA*

(Mollusca, Amphineura).

Region of investigation Great Barrier Reef, N.E. coast of Australia; tidal range springs 2.– metres, neaps 1.4 metres; investigator, Stephenson (1934).

During the Great Barrier Reef Expedition of 1928-29 one aimed among other things at procuring weekly samples of corals and of invertebrates other than corals to check their breeding activities. One of the species under observation was the chiton, *Acanthozostera gemmata*. Though a regular supply of Acanthozostera "became very difficult during the period of bad day tides in the summer" one succeeded in collecting enough samples to demonstrate that breeding started in the end of August, reached a height in the month of December, and died down in April. Mature specimen of both sexes were found at the end of the months, at the approach of full moon. Frequent sampling and isolation of single individuals in jars, and thus put out on the reef, showed that spawning took place exactly at the night of full moon. No spawning occurred in the jars in the nights immediately following or preceding full moon. The number of experiments and the quantity of animals used are too small, however, to establish once and for all that this species wholly confines spawning to the night of full moon and thus shows an extremely sharp maximum, not known in other species. One can feel assured, however, that Acanthozostera showed a marked lunar periodicity in breeding, with maxima about at full moon.

The following remark in Stephenson's report convinces us, that Acanthozostera belongs in our list of animals with nocturnal habits, highly sensitive to light, living in shallow water and showing a marked

periodicity in reproduction associated with periods of moonlit nights: "In the daytime the animals remain motionless in the crevices of the rocks, and underneath and on the shady parts of boulders, but at night can be found creeping about with surprising speed over the exposed surfaces."

Characterization: breeding period August-April, with its height in December. Narrowly limited spawning maxima, probably correlated with periods of moonlit nights, at full moon. Nocturnal habits.

The animals figuring in this list all show a marked periodicity in reproduction directly associated with the phases of the moon. The breeding season may vary from one month to all the year round, and maxima in spawning and swarming may vary in duration from one single night or day to about a fortnight, but all the species concerned have in common that a simultaneous maturation occurs, correlated with the periods of moonlit nights. Though the number of days required for egg-ripening may vary from place to place and from species to species, maturation is completed as a rule between full moon and last quarter, and at these phases of the moon spawning and swarming are located.

There is ample evidence that it is not the duration or the intensity of nocturnal illumination on the day of swarming itself which counts, but that swarming starts as soon as maturation is completed, be it, that several species select a special hour of the day or a special stage of the tide to perform their nuptial ceremonies.

The influence of nocturnal illumination on maturation should be understood by taking into consideration that the animals concerned live in shallow water in an area with a very modest tidal range (exceeding sensibly 1 metre only in the case of Acanthozostera gemmata), and that they, being highly sensitive to light, display nocturnal habits, living in a shelter during the daytime.

In case the breeding season is short and the maxima are clear-cut, reproductive activities are often concentrated to a very few hours a year, thus highly enhancing fertilization possibilities.

In the cases of *Eunice fucata* and *Platynereis dumerilii* it has been demonstrated, that tidal features may have some influence on the maturation process as well, respectively as a supplementary factor *(Eunice fucata)* and under different tidal conditions (Platynereis at Concarneau).

As in the animals showing maxima in reproduction associated with the sequence of springs and neaps, the key to a better understanding of these habits and to the influence of the external conditions is to make a clear distinction between breeding periods, maturation stimuli, and the conditions required for the swarming process itself, thus distinguishing a yearly, a monthly and a daily rhythm.

INCERTAE SEDIS

Here and there in literature we come across cases of periodicity in reproduction in marine animals,

about which we possess so far too little information to rank them decisively in one of our two lists. More information is required, and provisionally I enlist them here under the head "Incertae sedis," giving only a very concise description of the cases concerned.

1. *CENTRECHINUS SETOSUS*

(Echinodermata, Echinoidea).

Region of investigation Suez, Red Sea. Tidal range springs 1.2 metres, neaps 0.8 metres; investigator, Fox (1923, 1932).

Fox tried to find out whether or not a scientific base could be found for the popular belief, that the moon exerts an influence on reproductive activities in marine animals. He sampled quite frequently from communities of invertebrates at Suez (Red Sea) and at Alexandria (Mediterranean) and only found an apparent case of lunar periodicity in reproduction in the echinoid *Centrechinus setosus*, collected at Suez. Both in 1920 and 1921 he found two maxima in the percentage of mature animals at the approach of full moon in the summer season. We are therefore inclined to rank this case in our list of animals influenced by moonlight. Fox is aware that the intensity of the moonlight dwindles to insignificance compared with that of sunlight, but he points to the possibility that it is the number of hours of illumination, irrespective of its intensity, which counts, similar to that demonstrated, to be the case in maturation in birds. Perhaps we should presume that moonlight has an intensity above the threshold light value for the species concerned.

We know little about possible nocturnal habits in Echinoidea and about their sensitiveness to light I only found a very general remark in Brehm: "Eigentliche Sinnesorgane sind bei den Seeigeln unbekannt; doch ist die Haut ganz allgemein lichtempfindlich."

As Fox worked with quite modest numbers of animals, I prefer to rank this case provisionally among the incertae sedis.

2. *TOXOPNEUSTES VARIEGATUS*

(Echinodermata, Echinoidea).

Region of investigation Beaufort, North Carolina, on the Atlantic coast of U.S.A.; tidal range springs 0.9 metres, neaps 0.3 metres; investigator, Tennent (1910).

The breeding season of this echinoid extends throughout summer, being at its height during June and July. During the three summers preceding 1908 and again in 1908 Tennent noticed "that the gonads of sea urchins taken after a night of full moonlight were empty, while those obtained a week later gave an abundance of eggs and spermatozoa." No observations as to the habits of these sea urchins could be made for the reason that they were obtained from water in which the bottom could not be seen. Later on Tennent detected in shallow water at Tortugas, that individuals of Toxopneustes tend to gather more or less closely together when they are ready to spawn. This habit makes the collection of reliable samples from the entire population with the aid of a dredge, quite difficult.

Though we are inclined to rank Toxopneustes among the animals influenced in spawning activities by moonlight, it is better to wait till more is known about its nocturnal behavior, its sensitiveness to light and its congregational habits.

3. CONCHOPHTHIRIUS LAMELLIDENS Gosh.

(Crustacea, Copepoda parasitica).

Region of investigation fresh water ponds near Calcutta, India; no tidal influence; investigators, Ray & Chakraverty (1934).

This little parasite, living on the gills of the lamellibranch mollusc, Lamellidens marginalis Lam., appeared to show maxima in its conjugation about at the time of new moon. High peaks were observed in September, October, and November, 1933. In the month of December the peak shifted by five days. The authors try to explain this retardation by pointing to the arrival of the first cold wave in the season, a few days before the new moon. In January only a slight peak was observed, but in due time, at new moon, though a sharp drop in temperature occurred at the January new moon.

This is the only description of lunar periodicity in fresh water I came across. Tidal influence need not be taken into account. Before ranking this animal among those influenced by the light of the moon, I should like to learn how this tiny creature, living on the gills of a mollusc, perceives the difference between dark and moonlit nights.

4. PECTEN OPERCULARIS (L.)

(Mollusca, Lamellibranchiata).

Region of investigation Plymouth on the South coast of England; tidal range springs 4.8 metres, neaps 3.6 metres; investigator, Amirthalingam (1928).

Amirthalingam checked once a week samples (about 100 specimens) of queens *(Pecten opercularis)*, procured on trawling grounds about 40 metres deep, situated in the neighborhood of Plymouth. He sampled from February 1927 to March 1928 and his figures on the conditions of the gonads show reproductive activity from March to June, with maxima at about the time of full moon, the minima not dropping down to the zero level. The eggs developed in July and August were not spawned, but degenerated after the full moon. Amirthalingam checked the gut contents but found no perceptible difference in the course of the lunar cycle. As he made these observations several hours after actual feeding, animal matter may have been digested, meanwhile.[3]

Amirthalingam, in his efforts to analyze Pecten's breeding behavior, placed some queens in cages close to the sea bottom. In one cage sun- and moonlight could enter freely, in the second neither sunlight nor moonlight was allowed, in the third sunlight was admitted, but by covering the cage every night with a piece of canvas, the moonrays were shut out. The result was, that the differences appeared to be quite

[3] Mrs. Mansour-Bek of the Cairo University told me, that large quantities of small crustaceans, which use to swim in the surface layers of the sea at night, could be found in Tridacna's stomach, only if checked before dawn.

small, but the highest percentage of eggs was found in the third cage. This experiment has been carried out in August, however, after the closing down of the normal breeding season.

More evidence is required before this case can be classified. Some features point at tidal influence: (a) At Plymouth the tidal range is considerable and moreover the year under consideration showed quite a difference between full and new moon spring tides, so that preponderance of one of them is feasible in the rhythmical maturation of the eggs. (b) The samples were procured at a depth of about 40 metres, where moonlight is very scanty, indeed. (c) The experiment with the cages showed, that the queens in the cage which was hoisted and lowered at sunrise and sunset, exposing the molluscs to extra differences in water pressure, showed the highest percentages of eggs.

Other factors point to the possibility that moonlight interferes: Pecten is a mollusc equipped with a great number of eyes, consequently highly sensitive to light impressions. We should like to know more about the influence of light, at night and during the day, on its feeding behavior. The experiment with the cages was not carried out during the right part of the season, and moreover we are not convinced, that feeding conditions were quite normal in the cages.

5. PECTEN MAXIMUS (L.)

(Mollusca, Lamellibranchiata).

Region of investigation Port Erin, Isle of Man, Irish Sea; tidal range springs 5.4 metres, neaps 3.3 metres; investigator, Tang (1941); observations 1937-1938.

Tang sampled his pectens once a week or once a fortnight, each time about four dozen specimens. He found that the breeding season had its height from April to July. Though his investigations were mainly concerned with the annual cycle, Tang tells us, that "there are indications that a lunar periodicity similar to that found by Amirthalingam for *Aequi-Pecten opercularis*, may occur in *Pecten maximus*."

6. OBELIA GENICULATA (L.)

(Coelentrata, Hydrozoa).

Region of investigation Millport, Isle of Cumbrae, on the West coast of Scotland; tidal range springs 2.9 metres, neaps 1.8 metres; investigator, Elmhirst (1925).

Elmhirst tells us that he observed Obelia geniculata "giving off medusae during the ten-day periods beginning with the third week of the new moon in July, August and September" of the year 1924 "and not at other times." Miss Marshall found roundabout last quarter an occasional abundance of Obelia geniculata in the plankton. Colonies much eaten by nudibranchs may recover rapidly and reproduce at any time, "to which is probably due the fact that this case of lunar periodicity has escaped observation."

Though Obelia's photonastic qualities have been established, we are not informed about its displaying

nocturnal habits and it certainly does not take shelter during the daylight hours. Still it is conceivable, that here too it is the number of hours of illumination that counts, irrespective the intensity. More information, if possible of experimental nature, is required, before we can proceed to classify this case.

7. *LEPTONEREIS GLAUCA* Claparède

(Annelida, Polychaeta).

Region of investigation Concarneau, Brittany, France; tidal range springs 4.2 metres, neaps 2.1 metres; investigators Fage & Legendre (1923, 1927).

In the course of their frequent nocturnal sampling of invertebrates allured by artificial light, more amply dealt with above, Fage & Legendre caught some species of polychaete worms, only at a well-defined phase of the lunar cycle. Thus *Leptonereis glauca* was captured at the last quarter in May, June and July, while a big maximum of swarming in *Eulalia punctifera* Grube was repeatedly observed roundabout the last quarter of the August moon.

These captures and observations indicate that metamorphosis in these species is possibly influenced by moonlight. We should remember, however, that the tidal range is quite considerable at Concarneau and that the great majority of cases of moonlight calling forth maturation concerns animals living in water with a modest tidal range. This is no reason, however, to preclude the possibility of direct lunar influence on creatures living in a region with a great tidal range. More data are required before the principles of the rhythm in the species of polychaets concerned, can be corroborated satisfactorily.

8. *NEREIS LONGISSIMA* (Johnston)

(Annelida, Polychaeta).

Region of investigation Wimereux near Boulogne, Pas-de-Calais, France; tidal range springs 8 metres, neaps 4 metres; investigator, Gallien (1936).

Gallien executed some nocturnal pelagic fishing with the aid of a lamp in the Wimereux region, and caught among other animals, several times mature specimen of *Nereis longissima*. Though the numbers caught were quite modest, Gallien states that "l'essaimage s'effectue principalement au dernier quartier de la lune." It is possible that *Nereis longissima* should be ranked among the animals whose maturation is mainly governed by variations in nocturnal illumination, though living in a region with a considerable tidal amplitude. More data are required to establish this view.

9. *PERINEREIS CULTRIFERA* (Grube)

(Annelida, Polychaeta).

Region of investigations Cherbourg, Normandy, France; tidal range springs 7.– metres, neaps 4.– metres; investigator, Herpin (1925, 1928, 1929).

The results obtained by Fage & Legendre in their fine series of nocturnal sampling, instigated Herpin to carry out similar observations in the Cherbourg area. He soon found out that these waters certainly are less suitable for carrying through frequent sampling, for collecting large quantities of invertebrates.

and for witnessing swarming of polychaete worms. Strong and often even dangerous currents usually counteracted his efforts. In case only moderate numbers of animals are caught, one ought to be very careful in drawing conclusions. Especially negative results should be treated with great care, as swarming, often very restricted in space and time, is easily overlooked. This led Herpin (1928) to the following criticism on nocturnal observation: "Les pêches de nuit ne sont d'ailleurs pas exemptes de causes d'erreur. La pluie ou l'agitation de la mer peuvent empêcher ou retarder les essaimages en surface. Comme nous le verrons plus loin, ces essaimages sont des phénomènes très localisés, non seulement dans le temps, mais peut-être plus encore dans l'espace. Dans bien des cas il faudrait pouvoir faire des pêches tous les jours, dans la première et dans la seconde motié de la nuit, simultanément dans plusieurs stations de la même localité et aussi dans les localités éloignées." We understand how privileged Ranzi was in sampling in a restricted area without tidal currents and with prevailing fine weather.

Herpin found that the species living under the low water mark, showed as a rule the same swarming behavior as their congeners at Concarneau. Species living on the tidal flats, however, often showed quite another behavior and could sometimes even be observed to swarm during the daylight hours. This led Herpin to the statement "qu'il faut se défier des généralizations trop hâtives. Une même espèce peut avoir en diverses localités une biologie toute différente." Polychaets living very high on the tidal lands are forced to swarm during the short periods their habitat is immerged.

Herpin witnessed several times *Perinereis cultrifer* leaving its burrows in broad daylight, at first quarter between 2:00 p.m. and 4:00 p.m., immediately after the first slight immersion of their habitats. Fage & Legendre on the other hand, witnessed twice nocturnal swarming in this species at full moon. But "les essaimages de jour se distinguent par leur courte durée et surtout par l'absence de danses nuptiales." I believe that this kind of swarming should not be ranked among those cases previously discussed. Herpin demonstrated that the worms leaving their burrows appeared to be in different phases of maturation. This is in sharp contrast to the normal cases, in which we have seen, that only those individuals, which have completed maturation, join in swarming. Probably the very high temperature of the first flood water immersing the tidal lands on a bright afternoon in full summer, called forth the worm's abnormal behavior.

10. *CUMINGIA TELLINOIDES*

(Mollusca, Lamellibranchiata).

Region of investigation Woods Hole, Massachusetts, on the Atlantic coast of U.S.A.; tidal range springs 0.5 metres, neaps 0.3 metres; investigator, Grave (1927).

Grave checked spawning activities in the lamellibranch, *Cumingia tellinoides*, in the Woods Hole

area. The mechanical shock of removing the animals from their normal situation, furnished all the stimulus required to induce spawning under laboratory conditions. Grave states: "it was found that there is no perceptible stimulus from the opposite sex. They appear to spawn quite as readily when isolated as when in the same dish." Grave's figures clearly demonstrate, however, that those in the common dish spawned far closer together in point of time than the isolated individuals. Should not this be understood as an influence of a stimulus from the other sex?

Grave concludes that "the heaviest spawning occurs at the period of the full moon until new moon, the period of the first quarter is the period of restricted spawning." His data, presented in most unsurveyable protocols, from which it is impossible to produce a neat table, because of their heterogenity and their lack of exactitude, suffice, however, to demonstrate that important spawning was observed at first quarter as well (1-9-1922, 7-9-1924). Far more and better data are required before I am convinced that moonlight exerts an influence on maturation in a lamellibranch like Cumingia.

11. *NEREIS LIMBATA*

(Annelida, Polychaeta).

Region of investigation Woods Hole, Massachusetts, on the Atlantic coast of U.S.A.; tidal range springs 0.5 metres, neaps 0.3 metres; investigators, Lillie & Just (1913).

Lillie & Just collected many a night in the summer seasons of 1911 and 1912 and often caught mature individuals of *Nereis limbata* in great numbers. Their data do not show a very great regularity and this certainly is not a very clear-cut case of lunar periodicity. Important swarming was, however, always observed in the period between full and new moon. Sometimes the worms appeared in one big diffuse maximum lasting for about a week, sometimes in several maxima within the period mentioned. Sampling always took place after sunset and seldom or never in the second part of the night. The light of the full moon surpassed the threshold between positive and negative phototactical forces, for "swarming may begin after twilight and be suddenly cut short by the appearance of the moon above the eastern hills." On the other hand the authors tell us, that great swarms of the worm were allured by their lantern in dark nights. One should be careful in handling positive and negative influence of natural and artificial light on the results of sampling and observation. Sampling should always be practiced before moonrise or after moonset if comparable data are required. It is possible that *Nereis limbata's* maturation is influenced by the periods of moonlit nights in the Woods Hole region, with its modest tidal amplitude, but we need more reliable data to bear this out.

GENERAL IMPRESSIONS

It has literally been demonstrated in the foregoing, that periodicity in reproductive activities in inshore marine animals, is a world-wide feature. Several clear-cut cases of a rhythm in maturation and spawning correlated with the sequence of neaps and springs or with periods of dark and moonlit nights, have been discussed.

We can be sure, that a far greater number of inshore animals reproduce rhythmically in the course of their breeding season, but a great frequency of sampling is required to demonstrate this type of behavior. In regions with a considerable tidal range, the influence of the sequence of neaps and springs will most probably be found to preponderate, but there, where the tides are of little importance, invertebrates highly sensitive to light and displaying nocturnal habits, will more easily be influenced by the moonlight rhythm.

No doubt, concentration of reproductive activities to a short well-defined period within the tidal or lunar cycle is of great biological importance, greatly enhancing fertilization possibilities.

Particularly polychaete worms have been demonstrated to show a great many cases of periodicity in reproduction, and no doubt more of them will some time be shown to possess the same type of behavior. In Holland (Tholen) I witnessed e.g. dense swarming during broad daylight of our largest polychaete worm, *Nereis virens* Sars, exactly at new moon spring tide in April, 1946, but more observations are required to establish the principles of this rhythm.

Very frequent and quantitative observations in the field are necessary. The plankton studies carried through by Thorson (1946), for instance, however important and interesting they may be from other points of view, do not suffice to demonstrate whether or not the many species observed by him show a tidal or lunar rhythm in reproduction, as his samples were procured once in two or three weeks only.

Here and there in literature one can find indications of simultaneous spawning in inshore invertebrates. Thus Wiborg (1946) tells about the horsemussel, *Modiola modiolus* (L.): "men felles for alle skjellfelter er at gytningen kommer temmelig plutselig og kan være tilendebragt på mindre enn en dag."

Stimulation by the mutual sex products in Galtsoff's sense can help here and there to concentrate spawning, but first of all a simultaneous maturation is required. Galtsoff's principle has been demonstrated to work in several polychaetes too, but only during the very last part of the act, during the emission of the sex products in the nuptial dance. If this is the guiding principle in swarming itself, it should be very difficult to find a plausible explanation for the fact that the big maximum in swarming is usually preceded and followed by days with little or moderate swarming. In reality this phenomenon is caused by smaller differences in the number of days required for maturation.

The clue to a successful analysis of the once so mysterious lunar and tidal periodicity in the reproductive activities of inshore marine animals, is making a clear distinction between annual, monthly, and daily

rhythm. The annual rhythm, determines the length of the breeding season, varying according to the species and the area concerned from a fortnight to all the year round. Most probably temperature conditions preponderate in establishing the breeding season.

Within the breeding season a monthly rhythm may come into operation, either correlated with the sequence of neaps and springs or, in nocturnal species, by the alternation of series of dark and moonlit nights. It should be borne in mind, that it may occur, that full moon and new moon spring tide differ considerably in amplitude, thus causing a strong preponderancy of the one over the other. The monthly rhythm should be understood as a simultaneous egg-ripening in association with tides or moonlight. It is conceivable that in one and the same species the tides exert their influence in one locality, while moonlight preponderates in another situation; in rare cases both of them appear to co-operate.

The daily rhythm often sees to a simultaneous performance of the nuptial ceremonies at a well-defined hour of day or night, or at a well-defined phase of the tidal cycle. As in annual and monthly rhythm, the measure of concentration achieved by the daily rhythm differs highly from species to species.

Though field observations may still yield many a magnificent result in establishing rhythms in reproduction of marine animals, we eagerly await series of laboratory experiments to check the correctness of the theories and hypotheses discussed. Field observations on swarming not only are time-devouring and highly influenced by adverse weather conditions, but it remains difficult to judge what value should be attached to negative figures, as swarming is often very restricted in space and time. In laboratory experiments with sequences in rhythmical alternation of water pressure, differing in rhythm from those occurring in nature, and with different types of artificial illumination during the night, one should select species, which can easily be kept in perfect condition in the laboratory. Moreover one should aim at selecting species showing sharp maxima and zero minima in natural reproduction. Types like Spirorbis, Platynereis, and Chiton will do perhaps. One should bear in mind, that rhythmical impressions should be executed during several months in succession, as a certain sluggishness in adopting a rhythm other than that occurring in nature, is a common feature in biology.

SUMMARY

1. The production of oyster larvae in the Basin of the Oosterschelde (Holland) appeared to show a marked periodicity in the course of the breeding season.

2. Maxima in the production of oyster larvae can be expected to occur about 10 days after full and new moon. *Ostrea edulis* being an incubatory species, it can be inferred, that spawning shows its maxima at both of the spring tides.

3. One of the maxima in the production of oyster larvae preponderates, and that appeared to be situated between June 26 and July 10 in the years under consideration (1935-1946). Thus a reliable method for long term prediction of the greatest maximum in the production of oyster larvae could be established.

4. An analysis of the data on the production of oyster larvae showed that fluctuations in water temperature are of little or no importance in bringing about the periodicity in the course of the breeding season.

5. It could be demonstrated that it is highly probable, that it is the sequence of spring and neap tides, which calls forth rhythmical reproduction in the oyster, and that probably rhythmical differences in water pressure are the agent in this.

6. With the aid of the acquired knowledge on rhythmical reproduction in *Ostrea edulis*, it was possible to give a satisfactory explanation for many cases of so far badly understood periodicity in reproduction in animals other than oysters.

7. Periodicity in reproduction in the course of the breeding season, appeared to be called forth by the sequence of neaps and springs in those regions where the tidal range is considerable.

8. In areas with little or no tidal amplitude other factors could be held responsible for causing a rhythm in reproduction. In nocturnal animals, sensitive to light, the alternation of dark and moonlit nights appeared to be closely correlated with sexual maturation. Ranzi's data on Platynereis could be used as a basic case in our efforts to find a plausible explanation for similar cases of lunar periodicity, that of the famous Palolo worm included.

9. In order to analyze cases of periodicity in reproduction a clear distinction should be made between the annual rhythm (the length of the breeding season), the monthly rhythm (periodicity correlated with tidal sequence or lunar cycle) and the daily rhythm (concentrating spawning or swarming to a certain well-defined hour of the day, or to certain phases of the tidal cycle). In extreme cases these three rhythms in combination can see to a most complete concentration of reproductive activities in the species concerned, so that an entire population may spawn simultaneously during one single hour a year.

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